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PREFACE

This volume is the result of the encouraging reception accorded to our first volume. It is written along the same lines and with the requirements of the B. Sc. students constantly in view. It includes the various types of Bryophytes, Pteridophytes, and Gymnosperms prescribed for the B. Sc. course of the Indian Universities. All the life-histories are profusely illustrated and supplemented with the latest information on the subjects. Many standard books and journals have been drawn upon for the diagrams. They have been simplified to suit the understanding of the young reader. Some of them are also hypothetical. Care has also been taken to discuss each topic in as systematic a manner as possible. Mention must be made of photomicrographs which are a special feature of this volume.

Although a large number of life-histories have been included in keeping with the requirements of the B. Sc. course, we invite suggestions for the inclusion of others that may be deemed necessary.

Although we have tried to see that no typographical mistakes occur, we crave the reader's indulgence, if some have inadvertently crept in.

We acknowledge with thanks the help that we have received from the following scholars in the preparation of this volume ; Dr. S. Sinha of the Agra College, Prof. B. L. Gupta of the St. John's College, and Prof. S. N. Chaturvedi of the B. R. College, Agra ; Dr. Y. S. Murti and Dr. M. R. Sharma of the Meerut College, Meerut ; Prof. H. B. Saksena of the Victoria College, Gwalior ; Dr. S. C. Gupta of the D. S. B. Govt. College, Nainital ; Dr. A. S. Yadav of the Patna University ; Dr. S. C. Pandeya of the Science College, Raipur ; Prof. D. S. Loyal and Miss Ranbir Kaur of the Chandigarh University ; Lala Jamiat Rai of the Khalsa College, Amritsar ; Dr. A. P. Mehrotra and Prof B. B. L. Saksena of the K. N. Govt. Degree College, Gyanpur ; Dr. S. K. Roy and Prof. R. Sahai of the Gorakhpur University ; Dr. D. C. Bharadwaj of the Birbal Sahni Institute of Paleobotany, Lucknow ; Dr A. R. Rao of the Lucknow University ; Dr. V. V. Apte of the Fergusson College, and Dr. Y. B. Raje of the S. P. College, Poona ; Dr. K. B. Deshpande of

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Hyderabad ; Dr. J. Zacharia of the Wilson College, Prof. L. J. Dennis of the St. Xavier's College, and Dr. V. S. Rao of the Ram Narain Ruia College, Bombay ; and Dr. I. M. Rao of the Tirupati University.

Last but not the least we have been greatly aided by the advice and assistance given to us by our colleagues of the department of Biology to whom we are greatly indebted.

Department of Botany,
D. A. V. College,
Kanpur.

A. K. Saxena
R. P. Sarbhai

1. Gen
2. Hep
3. Ric
4. Mar
5. Ant
6. Ant
7. Mu
8. Spl
9. Eu
10. Fu
11. Br
12. Int
13. Ly
14. Ly
15. Se
16. Se
17. E

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CONTENTS

BRYOPHYTA

PAGE

CHAPTER I

1. **General Account of Bryophyta** 1

CHAPTER II

2. **Hepaticae** 7
3. Riccia—life history 10
4. Marchantia 21

CHAPTER III

5. **Anthocerotae** 33
6. Anthoceros—life history 33

CHAPTER IV

7. **Musci** 44
8. Sphagnum-life history 46
9. Eubrya 56
10. Funaria—life history 57
11. BIBLIOGRAPHY 76

PTERIDOPHYTA

CHAPTER V

12. **Introduction of Pteridophyta** 83

CHAPTER VI

13. **Lycopodiales** 91
14. Lycopodium—life history 91

CHAPTER VII

15. **Selaginellales** 110
16. Selaginella—life history 110

CHAPTER VIII

17. **Equisetales** 132
18. Equisetum 132

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CHAPTER IX

19.	**Pteropsida**	155
20.	Filicales	156
21.	Marsileales	157
22.	Marsilea—life history	157
23.	Pteridium—life history	175
24.	Osmunda ,, ,, ...	186
25.	Stelar system in ferns	198

SPERMATOPHYTA

CHAPTER X

26.	**Spermatophyta**	205

CHAPTER XI

27.	**Gymnospermae**	209

CHAPTER XII

28.	**Cycadales**	215
29.	Cycas—life history	217

CHAPTER XIII

30.	**Coniferales**	240
31.	Pinus	243

CHAPTER XIV

32.	**Gnetales**	265
33.	Gnetum—life history	266
34.	BIBLIOGRAPHY	282
35.	INDEX	i

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BRYOPHYTA

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CHAPTER 1

GENERAL ACCOUNT

Occurrence. Bryophytes occupy an important place in the plant kingdom although they are of little economic value. They have rightly been called the "amphibians of the plant kingdom" on account of their peculiar habit. Primarily they are terrestrial, though water is indispensible for them at one or the other stage. They include about 23,000 species which are cosmopolitan in distribution. They have a likening for shade and love for moisture.

The plants of this group belong to the temperate climate and occur more commonly in the rainy season. They are found on moist walls, on wet soil, on logs of wood, on tree trunks, near river banks, on river beds from where water has receded, on rocks and their crevices and at various other places. They may also occur as epiphytes. Their growth is gregarious and within a very short period they become so abundant as to occupy a big space though they never form a very conspicuous vegetation of a particular area. Some of the forms like *Riccia fluitans, Ricciocarpus natans* and *Reilla* are aquatic, but this is presumed to be an acquired character. A few species may be found on snow while others may occur in tropical regions. Sometimes the aquatic forms grow so abundantly in shallow ponds and pools that they cover the whole water surface forming a "quaking bog". *Liverworts* are confined to hills and other colder regions and are seldom found in plains while *Musci* are more widespread.

Size and form. They vary in form, although there is not much difference in their size. The plant body in *Hepaticae* (one of the classes of Bryophyta) is thallose or liver like. The thalli are branched, mostly prostrate and are attached to the substratum by means of rhizoids. In *Musci* (another class of Bryophyta) the plants are differentiated into rhizoids, stem and leaves. They are small in size, only a few centimeters in height. The tallest plant of this group is *Dawsonia* which reaches a height of 40 to 50 centimeters.

Important features. Bryophytes are regarded as the simplest and the most primitive land plants. They are presumed to be the first group of plants which have adapted themselves to the terrestrial conditions after being emerged from their aquatic habitat. Their aquatic ancestry

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is an established fact. Their important features may be enumerated as follows.

1. The plants are invariably green in colour. The plant body is thalloid in *Hepaticae*, while in *Musci* it is differentiated into rhizoids, stem and leaves.
2. Rhizoids are present in all the plants and their function is the same as those of the roots in case of higher plants, *i. e.*, fixation and absorption. They are thread like structures and may be unicellular or multicellular.
3. The internal structure of the stem in *Musci* is very simple. There is no well marked xylem and phloem in the conducting region. A few cells in the middle serve the function of conduction.
4. The plant body is a gametophyte. Reproduction is brought about by vegetative and sexual means.
5. The sexual reproduction is highly **oogamous** and takes place with the help of male and female organs of reproduction called the **antheridia** and the **archegonia** respectively. The former are club shaped while the latter are flask shaped. They develop on the mature plants. Each antheridium produces biciliate antherozoids and the archegonium possesses an egg.
6. Fertilization is brought about only in the presence of water and it results in the formation of an oospore which is retained in the archegonium.
7. There is no resting period and the oospore starts its germination immediately. Sooner or later the sporogonium differentiates into **foot, seta** and **capsule**. Sometimes seta may be absent and rarely foot may also be wanting. The sporophyte is more or less completely dependent on the gametophyte.
8. The capsule consists of spore mother cells contained in a spore sac or spore sacs. Haploid spores are produced from these diploid spore mother cells as the first division is reductional.
9. The spores thus formed are **homosporous,** get disseminated by wind and on reaching a suitable place germinate immediately. They produce protonemal branches which bear protonemal buds. The latter give rise to a new plant.
10. There are two clear generations in the life history of all the bryophytes. The stages before fertilization and after reduction division contain X number of chromosomes while the stages after fertilization and before reduction division contain $2X$ number of chromosomes. The former is called the **gametophyte generation** and the latter is known as the **sporophyte generation.**

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The two generations alternate with each other. This phenomenon is called the **alternation of generations.** It is a characteristic feature of this group.

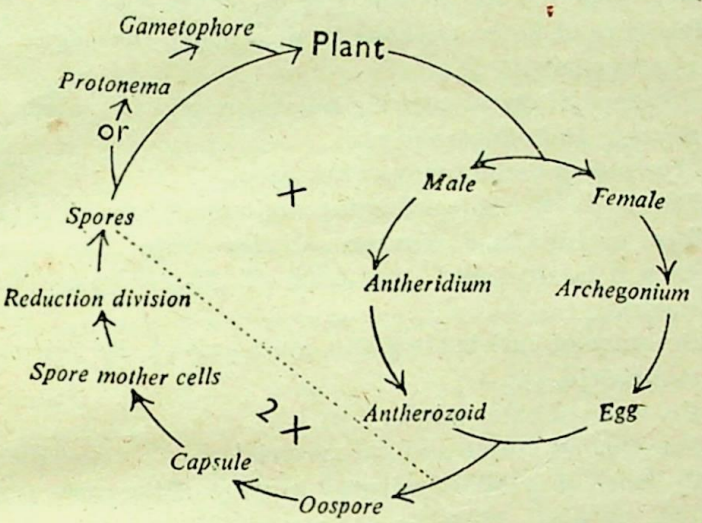

FIG. 1. Graphic life cycle of a Bryophyte showing alternation of generations.

Origin of Bryophytes. The plant body of the bryophytes is very soft and delicate and so one would not expect a fairly good fossil record to justify and establish their very correct origin. Walton (1925) found out *anacrogynous Jungermanniales* from middle carboniferous period, though he was not fully successful (1928) in establishing the presence of *Musci* in upper carboniferous. Arnold (1932) recorded the presence of *Sphagnum* leaves in cretaceous era.

With such a meagre fossil record and with practically no evidence of their immediate predecessors it is difficult to throw much light on this matter. However, botanists presume that bryophytes have originated either from pteridophytes or from algae. The different views expressed by the bryologists are summarized below.

1. **From Pteridophytes.** It is a mere speculation of certain bryologists that the group bryophyta has arisen from pteridophytes as a result of reduction. According to Lang (1917), Scott (1924), Halle (1936) and Haskall (1949) there are some similarities between the two groups. Their sex organs and sporophytes resemble each other. Kashyap supported this view.
2. **From Algae.** The theory of algal origin of bryophytes has the support of most of the workers. Though there exists a wide gap and also there is no direct link between the two groups, yet it is most probable that bryophytes might have originated

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from algae. There are a number of similarities between the two groups which are as follows.

a. Presence of ciliated antherozoids.

b. Necessity of water at the time of fertilization.

c. Presence of heterotrichous habit (among the algae in *Chaetophorales*).

d Presence of apical growing point (among the algae in *Phaeophyceae* and *Rhodophyceae*).

e. Presence of dichotomous branching.

f. Poorly developed conducting region (slightly thick walled cells form medulla in *Sargassum* and sieve tube like structures are present in advanced members of *Phaeophyceae* like *Macrocystis*).

g. Presence of cuticle (In algae, main axis of *Sargassum* possesses the cuticle).

h. Presence of chlorophyll.

i Presence of starch as food material.

j. Presence of cellulose cell wall in most of the cases.

On account of these similarities the two groups may be looked upon as near allies. The algal origin of the bryophytes is possible by gradual evolution. Lignier (1903) was the first to give some hint about this theory. According to him algae gave rise to *Prohepatics* which in their turn developed into bryophytes. Bower (1908) was the ardent supporter of this theory and according to him *Archegoniatae* originated from aquatic ancestors. The nearest ally of the bryophytes seems to be *Chlorophyceae*, the green algae, because the two groups bear many resemblances as already stated above. Fritsch also supported this theory and according to him *Chaetophorales* gave rise to bryophytes.

There are many others who believe and put forward evidences in support of this theory. Their belief is that the migration of algae from the water to the soil resulted in the formation of a reduced plant body. Most probably the plants first grew in abundant moisture and so only rhizoids developed in the beginning instead of roots. Therefore conducting system also remained poorly developed. The structure and method of gametic union are clear evidences of very much moist conditions prevailing at the time of transmigration.

So it is not very difficult to see the gradual evolution of bryophytes from algae. The trouble arises when we note the difference in the structure of the sex organs. The explanation for it is that the sex organs, the male and the female called the antheridia and the archegonia respectively, have been evolved by the sterilization of the outermost layer of cells of a multicellular gametangium like the one found in *Ectocarpus*. Again the difficulty is that the multicellular gametangia are unknown in *Chlorophyceae*, the group from which bryophytes are supposed to

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have originated. But according to Smith (1938) reproductive cells of *Schizomeris* and antheridia of *Chaetonema* (both green algae) resemble with the gametangia of *Ectocarpus*.

According to Church fresh water forms have nothing to do with the origin of land plants. The ancestors of the land plants, according to him, are marine forms. But his theory has not been supported by any fossil or geological record. All the more it is almost an established fact that if at all the algae are the ancestors of the land plants, they are the members of *Chlorophyceae*, a class which rarely inhabits sea. Therefore his theory loses its significance. According to Richards (1959) these relationships are not supported by well established fossil records and therefore satisfactory conclusions cannot be derived. There is, however, one very important character in the bryophytes which carries this group near to algae and that is the resemblance of their protonemal stage to the filamentous algae. Anyhow if there is any affinity between the two groups, it is remote.

Classification of Bryophytes. Braun (1864) was the first to include *Algae, Fungi, Lichens* and *Mosses* in Bryophyta. But as we know only *Mosses* form a class of Bryophyta, while the former three comprise a separate group—*Thallophyta*. Eichler divided the bryophytes into two classes—*Hepaticae* and *Musci*. Many workers like Bessey and Bower followed the same classification. Schiffner (1893) also divided bryophytes into *Hepaticae* and *Musci*. Some bryologists follow the same classification even now.

Underwood (1894) made a minor modification by taking out *Anthocerotales* from *Hepaticae*. Gayet (1897) gave *Anthocerotales* the rank of a class and Howe (1899) favoured and recognized this proposal. He simply changed *Anthocerotales* to *Anthocerotes*. Cavers in 1911 ("New Phytologist."—"The interrelationships of the Bryophyta") completely dropped the words *Hepaticae* and *Musci*. His system of classification may briefly be mentioned below.

1. *Sphaerocarpales*.
2. *Marchantiales*.
3. *Jungermanniales*.
4. *Anthocerotales*.
5. *Sphagnales*.
6. *Andreaeales*.
7. *Tetraphidales*.
8. *Polytrichales*.
9. *Buxbaumiales*.
10. *Eubryales*.

This system of classification was not favourably received by many workers. Dixon (Student's hand book of the British Mosses) and Mac Vicar (Student's hand book of the British Hepatics) in 1896 and 1912 respectively, retained the two groups (*Hepaticae* and *Musci*)) and later on

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Dixon and Verdoorn (1932) in "Manual of Bryology" confirmed this classification.

Now bryophytes consist of three classes—*Hepaticae, Anthocerotes* and *Musci*. This classification has been followed by Campbell, Smith and Takhtajan, but they spell *Anthocerotes* as *Anthocerotae*. The classification of Smith (1955) has been followed in this book simply for the sake of convenience.

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CHAPTER 2

HEPATICAE

It includes about 175 genera and 8,500 species. *Hepaticae* in Latin means liver. According to "Doctrine of Signatures" the medieval herbalists called this group *Liverworts* on account of its supposed value as a remedy for liver troubles. It may be just for the fanciful resemblance of the thallus lobes of the members of this group to the lobes of the human liver.

The plant body in liverworts is a gametophyte which may be thallose or foliose. When thallose it is prostrate and dorsoventrally differentiated. Stem and leaves are lacking. Rhizoids and scales are present on the ventral surface. Rhizoids are smooth walled and tuberculate. The foliose forms resemble mosses but can readily be distinguished from them on the basis of the following characters.

The foliose *Hepaticae* are prostrate and bear two or three rows of leaves while in the case of *Mosses* there are many rows of leaves spirally arranged. The leaves in the latter class possess a mid-rib while no mid-rib exists in the former one. The rhizoids are without any septa in leafy *Liverworts* while those of *Mosses* possess distinct oblique septa.

The sporophyte of *Hepaticae* is completely dependent on the gametophyte. The capsule possesses spores and may also contain sterile cells —the **elaters**. It may be differentiated into foot, seta and capsule.

Classification of Hepaticae. Many years back there was a lot of controversy regarding the classification of *Hepaticae*. Formerly this class had only two orders—*Jungermanniales* and *Marchantiales*. Later on Cavers (1910) added another order *Sphaerocarpales* which formerly had the rank of a family, *Sphaerocarpaceae* of *Jungermanniales*. Campbell (1936) raised the family *Calobryaceae* of *Jungermanniales* to the rank of an order *Calobryales*. Thus four orders are recognized in this class (Smith, 1955).

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1. *Calobryales.*
2. *Jungermanniales.*
3. *Marchantiales.*
4. *Sphaerocarpales.*

MARCHANTIALES

The order includes about 30 genera and 400 species. The plant body is prostrate, ribbon shaped, dichotomously branched and exhibits dorsoventral differentiation. Generally the dorsal side has well marked photosynthetic region and air chambers which open to the outside. The ventral surface of the thallus does not show any differentiation of tissues but is simply composed of parenchymatous cells which form a storage region. Rhizoids of smooth and tuberculate type are present on this side. Scales also occur on the same surface.

The sex organs are borne either directly on the dorsal surface or on special branches. The sporophyte varies in structure. Either it possesses only a capsule (*Riccia*) or may be differentiated into foot, seta and capsule (*Marchantia*). The spores may or may not be associated with the sterile cells (elaters). The sporophyte, therefore, may be simple or complicated.

Classification of Marchantiales. Different classifications have been put forward from time to time by different bryologists. They may be summarised as follows.

Schiffner (1909) and a few others recognized only two families in the beginning.

1. *Ricciaceae.*
2. *Marchantiaceae.*

Goebel supported this classification. Lotsy added one more family and so according to him there are three families.

1. *Sphaerocarpaceae.*
2. *Ricciaceae.*
3. *Marchantiaceae.*

Campbell also recognized three families but he differed from Lotsy. According to him the families are.

1. *Ricciaceae.*
2. *Corsiniaceae.*
3. *Marchantiaceae.*

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Cavers (1911) classified the order as follows.

1. *Ricciaceae.*
2. *Corsiniaceae.*
3. *Targioniaceae.*
4. *Monocleaceae.*
5. *Marchantiaceae.*

Verdoorn (1932) gave the following classification.

1. *Marchantiaceae.*
2. *Operculatae.*
3. *Astroporae.*
4. *Targioniaceae.*
5. *Corsiniaceae.*
6. *Ricciaceae.*

Evans (1939) also recognized six families but his families were different from those of Verdoorn's.

1. *Marchantiaceae.*
2. *Rebouliaceae.*
3. *Sauteriaceae.*
4. *Targioniaceae*
5. *Corsiniaceae.*
6. *Ricciaceae.*

Campbell (1940) made amendments in his earlier classification and finally approved of five families.

1. *Ricciaceae.*
2. *Corsiniaceae.*
3. *Targioniaceae.*
4. *Monocleaceae.*
5. *Marchantiaceae.*

This classification has been followed by Smith (1938, 1955) and it has also been incorporated in this book.

RICCIACEAE

The family includes three genera and about 140 species. It has the simplest type of sporophyte which is not differentiated into foot, seta and capsule. The spores are not mixed up with elaters. The gametophytic plant body is simple with the ventral parenchymatous region and a

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dorsal assimilatory portion where cells form longitudinal filamentous chains. Out of the three genera (*Oxymitra, Ricciocarpus* and *Riccia*), only *Riccia* will be discussed.

Systematic Position

Bryophyta.
Hepaticae.
Marchantiales.
Ricciaceae.
Riccia.

Occurrence. It is a common widely distributed genus and includes about 130 species. All the species are terrestrial except the one, *R. fluitans* which is aquatic and is found in free floating condition. Other species inhabit moist places like banks of streams, tree trunks, wet walls, rocks and beds of rivers from where water has receded.

In undivided India, Kashyap reported a number of species from Lahore, Pathankot, Manali, Kulu, Simla and various other regions of Western Himalayas. Rangachariar and Tirunarayanan reported *R. himalayensis* from Tinnevelly Hills and Darjeeling respectively. This species can be found upto a height of 9000 feet *R. robusta* is traceable upto 13000 feet and has been reported by Pande and Singh. Some other species have been reported by Qizilbash from Peshawar, by Hora from Manipur and by Iyengar from Madras. Chopra reported 14 species of *Riccia* from India. Recently there has been more addition in the new species of *Riccia* from this country. These are, *R. Kashyapii* by Kachroo (1954), *R. personii, R. Arnellii, R. benghalensis* by Khan (1957), *R. Aravalliensis, R. tuberculata* by Pande and R. Udar (1957, 1958), *R. Pandei* by R. Udar (1958) and *R. Pimodii* by Kachroo (1959).

S. Ahmad (1942) reported three species—*R. orientalis* Ahmad (a ciliate species), *R. gangetica* Ahmad (a monoecious species) and *R. mangalorica*. The latter species, according to the same author, may be a variety of *R. plana* Tay.

Ricciocarpus natans is an allied genus and is found in free floating condition. This species, as well as the aquatic species of *Riccia*, may grow in the terrestrial habitats also, but under such conditions their shape changes so much that it is rather difficult, though not impossible to recognize them.

According to Kashyap *R. himalayensis* is the only species which gets infection of an *Ascomycetous* fungus. The perithecia of this fungus may be mistaken for the capsules of *Riccia*.

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Structure. The plant body is in the form of a delicate, ribbon-like dichotomously branched thallus. The aquatic species are, thin, membranous and light green while the terrestrial ones are comparatively thick and dark green. The thallus often becomes rosette shaped (Fig. 1.) on account of the repeated dichotomy. It is prostrate and dorsoventrally differentiated. On the dorsal surface the thallus exhibits a thick and very conspicuous mid-rib (Fig. 2). There is a depression in the apical portion which forms a notch, where the growing point is located.

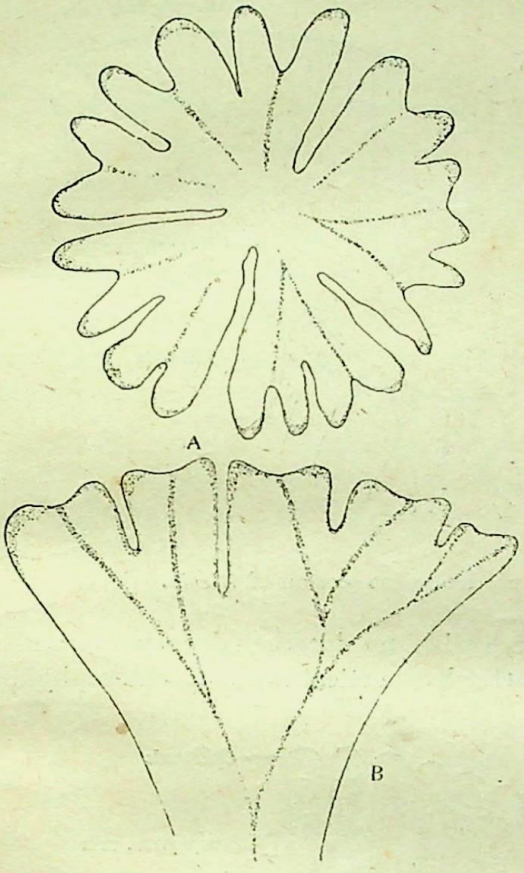

FIG. 2. External features of *Riccia* thallus. A, a group of thalli. B, dorsal side of the thallus.

Scales and rhizoids are present on the ventral surface. The scales are multicellular and violet in colour. They are crowded near the growing apex, and are meant for its protection. They are situated in one row near the apical portion, but the row seems to become double in the posterior region of the thallus. It is due to the splitting of the median line which also breaks up the scales and so they seem to be in two rows, one near each lateral margin. The scales may disintegrate in aquatic species while they may be persistent in the case of terrestrial ones.

The rhizoids are situated on the ventral side of the thallus. They are analogous to the roots of higher plants, that is, their function is also fixation and absorption. They are of two types—smooth and tuberculate. The former are long unicellular structures while the latter ones have outgrowths arising from the inner surface of their walls. The hygrophilous species may be devoid of such structures.

The detailed anatomical study may be made in a vertical cross section of the thallus. It is differentiated into two clear regions—a colour-

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less parenchymatous region on the ventral side and a chlorenchymatous portion on the dorsal side (Fig. 3.) The former consists of compact

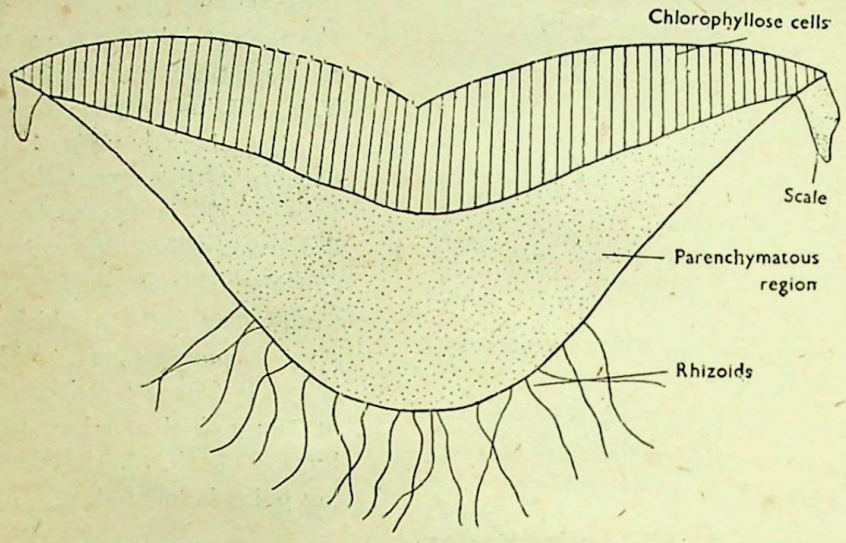

FIG. 3. Topographic vertical cross section of *Riccia*.

parenchymatous cells having starch with no intercellular spaces and is called storage region while the latter has vertical rows of chlorophyllous

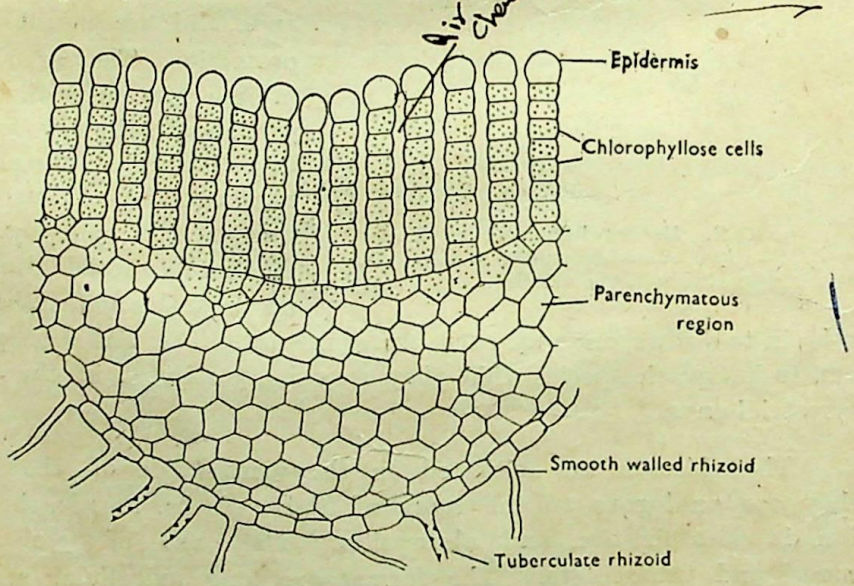

FIG. 4. Vertical cross section of *Riccia* thallus showing detailed anatomy.

cells separated by air chambers and is known as assimilatory region. The epidermis of the ventral surface is continuous having rhizoids and

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scales. The epidermis on the dorsal side is discontinuous and is single layered The air pores are meant for the exchange of gases (Fig. 4). In aquatic species like *R. fluitans* the epidermis may be continuous. The growth of the thallus takes place by a single apical cell situated in the apical notch.

Reproduction. It takes place by two methods.

1. *Vegetative.*
2. *Sexual.*

1. **Vegetative.** The vegetative reproduction takes place by any of the following methods.

A. As the plant matures, there is death and decay of the older parts. The decay continues till it reaches dichotomy when the surviving branches become separated and grow as two new individuals.

B. According to Smith, the plants cannot withstand the summer drought and during this period they are killed except their growing apices. On the return of the favourable conditions these apices again grow out into new plants.

C. According to Cavers (1903), many species grow by adventitious branches which may be formed on the ventral surface of the thallus. On being detached these branches give rise to new plants *e. g.*, in *R. fluitans.*

D. According to Goebel, in certain species tubers also help in vegetative reproduction. These tuber like structures have been observed in *R. vesicata* and *R. bulbifera.*

E. Fellner (1875) reported the formation of a new thallus from the apex of a rhizoid in case of *R. glauca.* Campbell (1928) reported that there are cell divisions in the apex of rhizoids which result in the formation of gemmae like structures. They also give rise to new plants.

F. In some species apex of the thallus grows down into the soil at the end of the growing season and becomes thick. On the return of the favourable conditions it grows out into a new plant.

2. **Sexual.** The sexual reproduction takes place with the help of male and female organs of reproduction called antheridia and archegonia respectively. They are produced on the gametophytic plant body. Some species may be monoecious as *R. crystallina, R. robusta, R. frostii, R. glauca, R. pathankotensis* while others like *R. discolour, R. himalayensis, R. sanguinea, R. Bischoffii* and *R. curtisii,* are dioecious. The development of the sex organs starts as soon as the plants are mature. They are produced on the dorsal side of the thallus and are arranged in acropetal succession. Side by side there is also an activity in the neighbour-

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ing vegetative tissue which surrounds the sex organs. It results in the formation of chambers, and each sex organ lies enclosed at the bottom

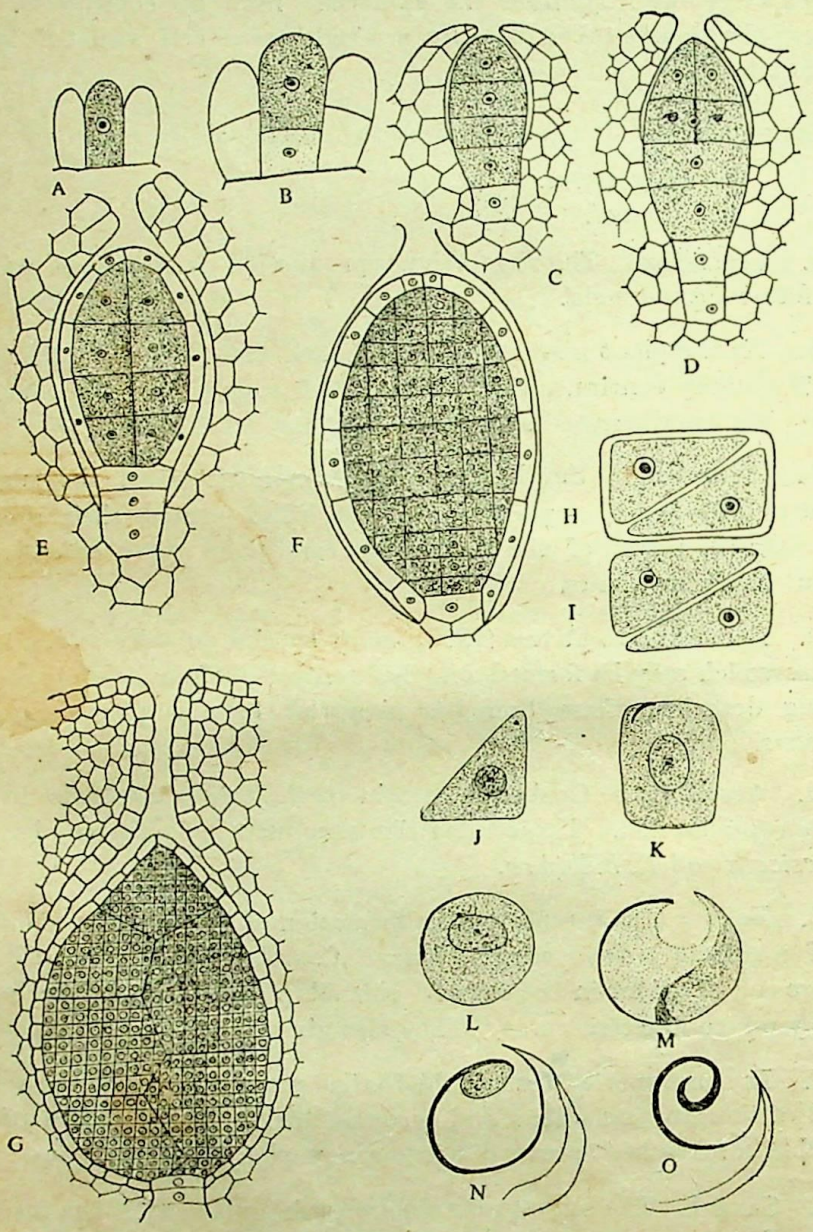

FIG. 5. Development and structure of an antheridium of *Riccia*. A, antheridial initial. B, transverse division of the antheridial initial. C, four celled antheridium. D, E, appearance of vertical wall and periclinal divisions forming the antheridium and jacket layer. F, antheridium with a short stalk and androgonial cells. G, antheridium, fully mature containing antherozoids. H-O, stages in the development of an antherozoid from an androcyte.

of such a chamber. However, the archegonia are never completely surrounded by this tissue, as their necks come out of the chamber.

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Development of antheridium. Black (1913) and Campbell (1918) investigated the development of the antheridium and according to them it develops from a single superficial cell, which forms the **antheridium initial** (Fig. 5, A). The latter lies slightly away (hardly two or three cells away) from the apical initial. It now enlarges and then divides transversely into two, a **basal cell** and **an outer** cell (Fig. 5, B). The former remains embedded in the vegetative tissue, while the outer cell emerges out from the thallus though slightly. The basal cell further divides and finally forms the embedded portion of the stalk of the antheridium, while the antheridium proper is formed by the outer cell. The latter divides and gives rise to a row of four cells which are more prominent than the basal cell (Fig. 5, C.).

Out of these four cells so formed, the two upper ones are called primary antheridial cells and the lower ones are known as primary stalk cells. As the name indicates the primary stalk cells develop the stalk and the primary antheridial cells give rise to the antheridium. Now two successive vertical walls are laid down in both the primary antheridial cells at right angles to each other (Fig. 5, D.) forming two tiers of four cells each. At this stage the periclinal walls are also laid down in both these tiers of four cells with the result that eight sterile jacket cells are formed, which surround a group of eight fertile primary androgonial cells (Fig. 5, E).

The jacket cells further divide by anticlinal divisions resulting in the formation of a single layered multicellular **sterile jacket** which surrounds the developing antheridium (Fig. 5, F). In the meantime the primary androgonial cells undergo many divisions giving rise to smaller **androgonial cells** (Fig. 5.) The last generation of the latter cells is termed the **androcyte mother cells.** These mother cells divide diagonally and finally each androcyte mother cell gives rise to two **androcytes** (Fig. 5, G). The latter are triangular in shape in the earlier stages, but later on they become spherical. Each androcyte forms a single antherozoid (Fig. 5, H–O) which is uninucleate and biciliate.

A mature antheridium consists of a small stalk and a globular or club-shaped body with a round or conical apex. The cell walls within it also disintegrate and finally all the antherozoids lie in a single cavity surrounded by the cells of the sterile jacket. When water enters the cavity, it softens. The cells of the sterile jacket ultimately break down and antherozoids come outside along with the mucilaginous substance. The antherozoids find their way outside on the dorsal surface of the thallus.

Development of archegonium. It also develops from a superficial cell which lies slightly away from the apex (hardly two or three cells

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away). This cell forms the **archegonium initial** (Fig. 6, A). Soon it divides into two by a transverse division, a **basal cell** and an **outer cell** (Fig. 6. B). The latter gives rise to the body of the archegonium while the former develops only its embedded portion. The outer cell divides

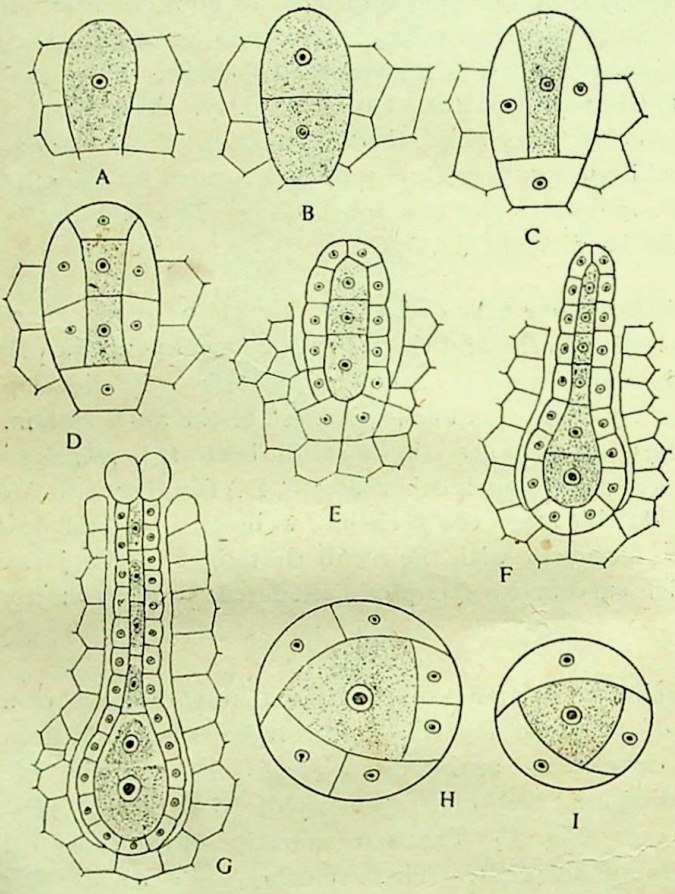

FIG. 6. Development and structure of an archegonium of *Riccia*. A, archegonial initial. B, transverse division of the archegonial initial. C, formation of three vertical walls and appearance of primary axial cell in a L. S. D, F, stages in the development of a mature archegonium. G, a mature archegonium with a swollen venter and a long neck. H, six neck initial surrounding a neck canal cell in a T. S. I, primary axial cell surrounded by three walls.

by a vertical division followed by two more such divisions resulting in the formation of four cells, out of which three are peripheral and one is median (Fig. 6, C). These cells are placed in such a way that the three peripheral initials lie lateral to the fourth one which is called the primary axial cell. The four cells can be seen in a cross section (Fig. 6, I). Each peripheral cell now divides vertically to form six jacket initials (Fig. 6, H) while the primary axial cell divides to give rise to an upper primary cover cell and a lower central cell (Fig. 6, D).

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Now the six jacket initials divide transversely to form two tiers of six cells each. The upper tier is called the **neck initial** and the lower tier is known as **venter initial.** The neck initials divide transversely to form a neck six to nine cells in height. The number of vertical rows of neck cells is an important feature of this order. There are six rows of neck cells in *Marchantiales*. On the other hand the six venter initials divide repeatedly forming a **venter** of twelve to twenty cells. The divisions are both transverse and vertical.

At the same time, primary cover cell also divides by two vertical divisions at right angles to each other and gives rise to four cover cells. The central cell divides by a transverse wall to form an upper primary neck canal cell and a lower primary ventral cell (Fig. 6, E). The former further divides transversely to form usually four neck canal cells while the latter divides by a transverse division to give rise to a ventral canal cell and an egg cell (Fig. 6, F).

Thus an archegonium, when fully mature, is a flask-shaped structure with a long neck and a swollen venter. At the top of the neck there are four cover cells which are broader than the neck cells. The neck has six to nine tiers of cells arranged in six vertical rows. The swollen venter is composed of twelve to twenty cells. Within the neck are four neck canal cells and the venter consists of one ventral canal cell and an egg (Fig 6, G).

Fertilization. Water is indispensable for fertilization as it not only helps in the transference of sperms but also causes the neck to open. The dorsal furrow which contains rain water or dew acts as a capillary tube. The presence of water in this furrow is quite sufficient to facilitate the movement of the antherozoids.

At the same time the neck canal cells and the venter canal cell within the archegonium also disorganise and a mucilaginous mass is formed which absorbs water (Fig. 7, A). The whole mass now swells and creates a pressure on account of which the cover cells separate from each other, thus leaving a clear passage for the entry of the antherozoids. Now the free swimming antherozoids reach the neck of the archegonium, pass downwards, and reach the nucleus of the egg. Finally the nucleus of the male unites with the nucleus of the female resulting in the formation of an oospore (Fig. 7, B).

Post fertilization stages. Soon after fertilization the oospore forms a wall round itself, enlarges in size and finally occupies the whole cavity of the venter. Simultaneously the cells of the venter undergo periclinal divisions. Anticlinal divisions also follow and ultimately two layered calyptra is formed having a young sporophyte inside (Fig. 7, D–F).

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At the same time the oospore also divides into two equal cells (Fig. 7, C). It is soon followed by a second division at right angles

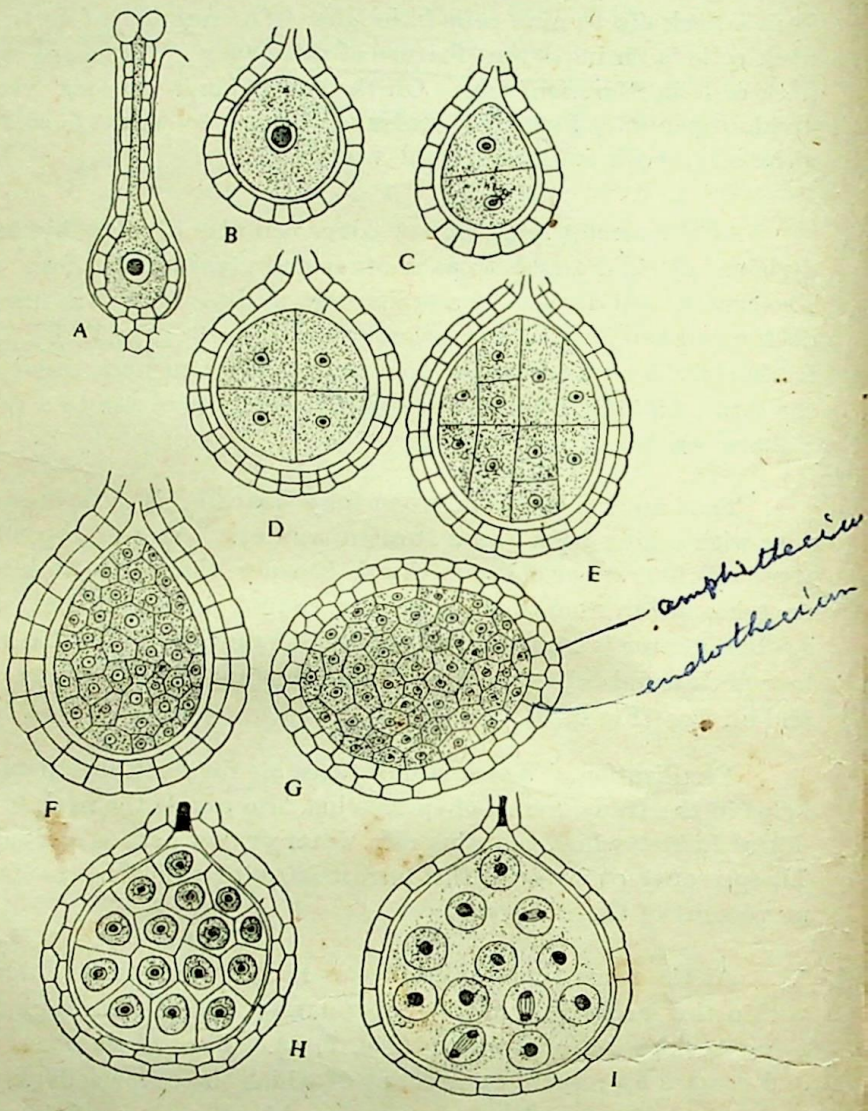

FIG. 7. Fertilization and post fertilization stages in *Riccia*. A, egg before fertilization. B, oospore just after fertilization. C, first division in the oospore. D, second division in the oospore. E, more divisions in young sporophyte. F, G, differentiation of amphithecium and endothecium. H, spore mother cells. I, reduction ivision in spore mother cells.

to the first resulting in the formation of a quadrant. (Fig. 7. D). Occasionally the second division may also be parallel to the first and so instead of a quadrant a filament like or a linear four celled embryo is formed. According to Lang (1905) both types of embryos may be found

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in the same genus. One more vertical division at right angles to the already formed walls gives rise to an eight celled embryo.

Many more divisions follow but they are all irregular. When the embryo consists of 20–40 cells, periclinal divisions are laid down. This results in the formation of an outer layer called **amphithecium** and an inner layer known as **endothecium** (Fig. 7, G). The former is merely a sterile jacket meant for the protection of young embryo while the latter is archesporium which divides repeatedly forming sporogenous cells. The last generation of the latter cells is called spore mother cells or sporocytes (Fig: 7, H.) The mother cells sooner or later divide twice to form spores. The first division is reductional, which puts an end to the sporophyte generation (Fig. 7, I).

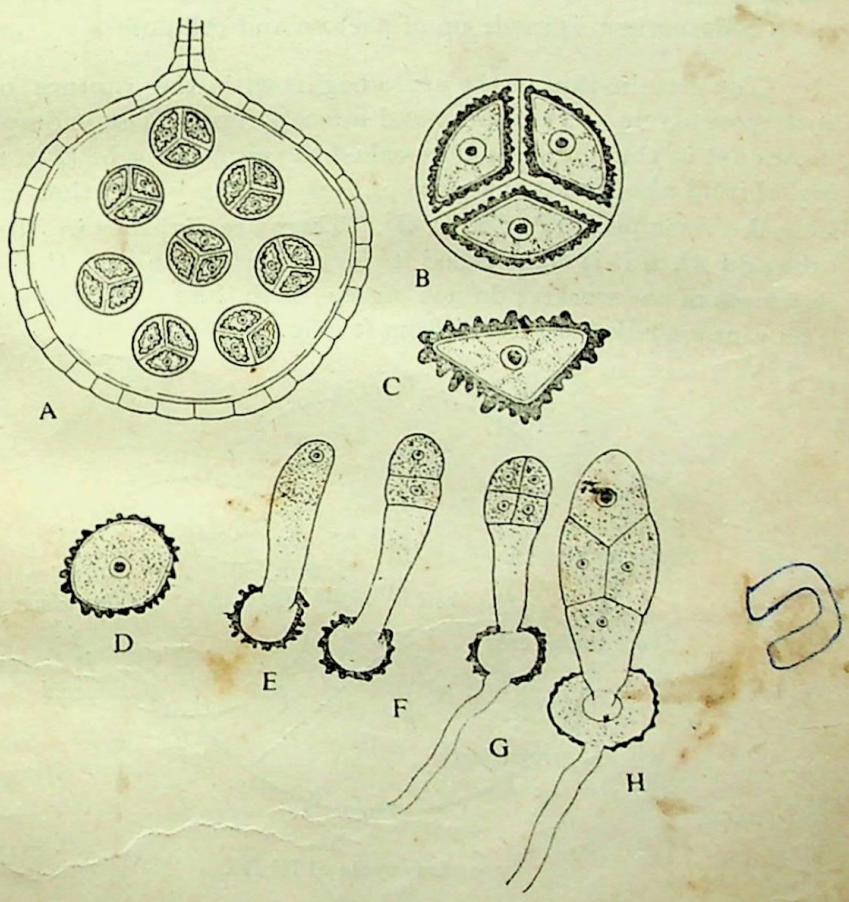

FIG. 8. *Riccia*. A, mature capsule or sporogonium containing tetrads of spores. B, a spore tetrad. C, a spore showing thick walled exosporium. D.—H, stages in the germination of the spore and formation of a new thallus.

The four spores so formed are tetrahedrally arranged (Fig. 8, B) and remain embedded in a common sheath which is more or less spheri-

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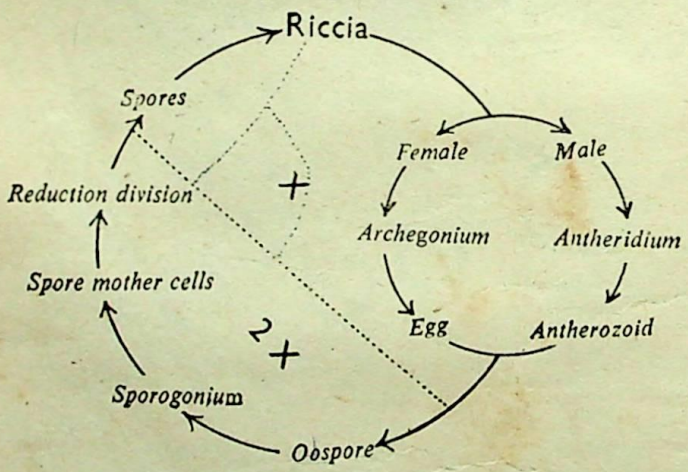
cal (Fig. 8, A). The spores remain in it till maturity. According to McAllister (1916), in *R. curtisii* the spores may not separate at all even after maturity and so they are disseminated *en masse*. There is no special method for the liberation of the spores. They are set free to the outside simply by the death and decay of the thallus. This process may take a long time.

Structure and germination of the spore. A fully mature spore is uninucleate and is more or less pyramidal in shape. It has an irregular thickening and is made up of three layers of walls which are easily distinguishable (Fig. 8, C). According to Beer (1906) the outermost layer is **exosporium** which is highly cutinized, the middle layer, **mesosporium** which has got three concentric layers, is also cutinized and the innermost, **endosporium**, is made up of pectose and cellulose.

The germination of the spore begins with the rupture of the two outermost layers—exosporium and mesosporium. The endosporium protrudes out in the form of a tube called the germinal tube (Fig. 8. E). The first rhizoid also comes out more or less at the same time and nearly from the same place (Fig. 8, F, G). There are divisions in the germinal tube and when it is eight celled it is called protonema (Leitgeb 1879). But most of the workers do not agree with him. Anyhow, sooner or later a new thallus is formed from it (Fig. 8, H).



Life cycle of *Riccia*.

MARCHANTIACEAE

The family includes about 23 genera and 250 species. The genera of this family are characterized by the presence of archegoniophore which bear archegonia, the female organs of reproduction. A very important genus of this family *Marchantia* possesses even antheridiophores which bear antheridia, the male organs of reproduction. Another

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characteristic feature of the family is the presence of sterile cells, the elaters within the capsule.

Systematic position

Bryophyta.
Hepaticae.
Marchantiales.
Marchantiaceae.
Marchantia.

Occurrence. Known even today by its first name given to it in the 18th century by a French botanist Marchant in memory of his late father

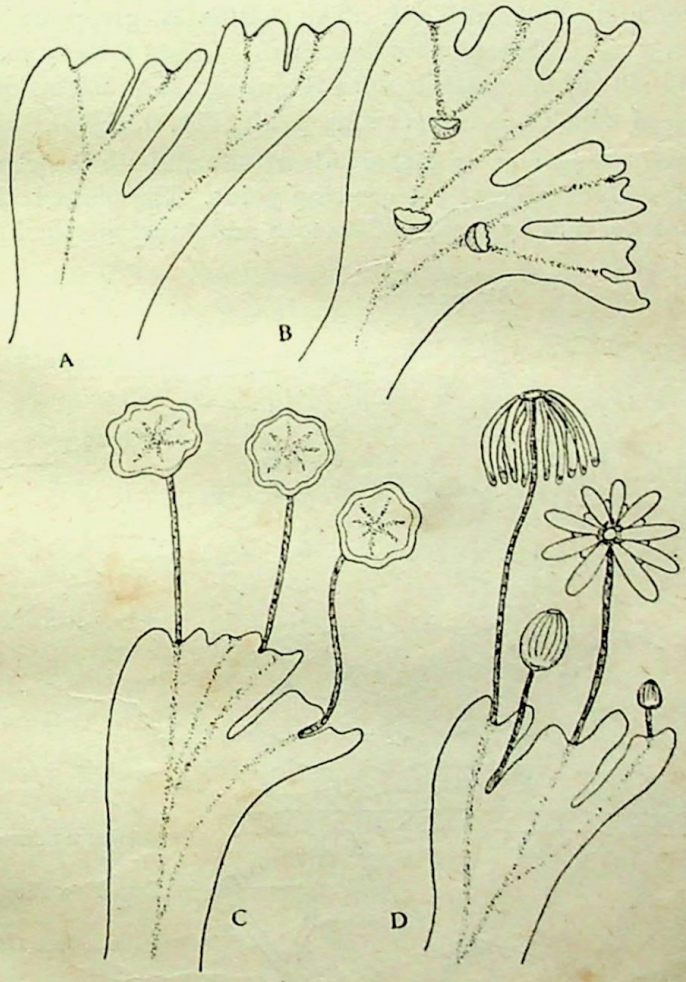

FIG. 9. *Marchantia*. A, dorsal view of the thallus. B, thallus with gemma cups. C, thallus with antheridiophores. D, thallus with archegoniophores.

who was the director of the Duke of Orlean's Garden in Blois, *Marchantia*

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includes about 65 species which are all cosmopolitan in distribution Kashyap has reported four species from India ; *M. polymorpha, M. palmata, M. nepalensis* and *M. Simlana*. The plants are usually found in cold, moist and shady places or in open woodlands. They may be found near the banks of streams and damp places. *M. palmata* has been reported from Ootacamund (Nilgiris) and Srinivasan has worked out its detailed life history. It is also fond of places where there have been fires, perhaps on account of the fact that active nitrification follows in the soil just afterwards. In 1929 after a big fire at Wicken Fen (Near Cambridge) *Marchantia* grew abundantly and covered the whole burnt peat.

Structure. The gametophytic plant body of *Marchantia* is prostrate and dorsoventrally differentiated. The thallus is green or dark green in colour and is dichotomously branched. It has a wavy margin with a distinct mid-rib which extends upto the apex. The latter has a notch, at the base of which lies the growing point (Fig. 9, A).

The ventral surface on either side of the mid-rib bears two or more rows of scales which protect the growing point. The plant body is attached to the substratum by means of smooth and tuberculate rhizoids.

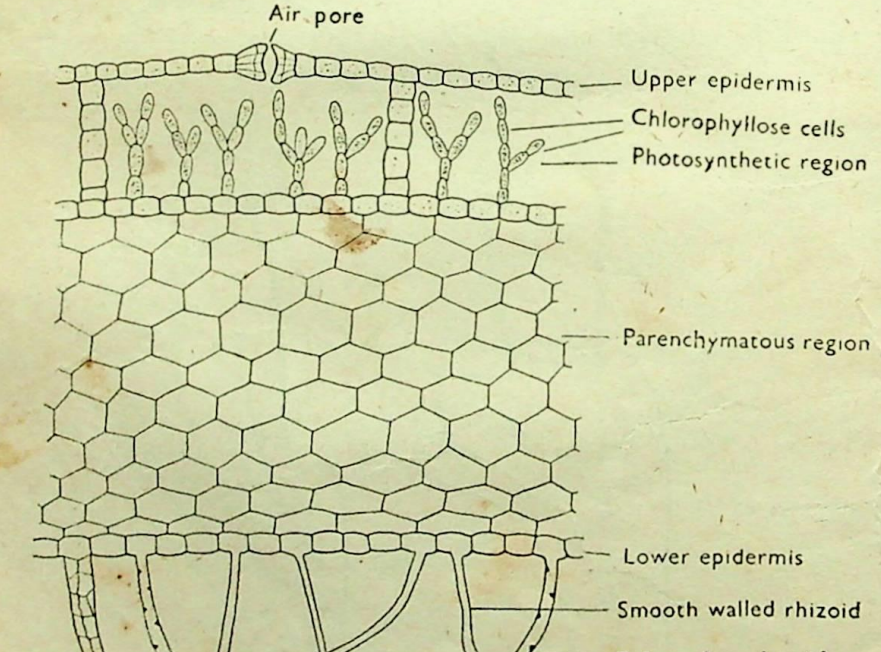

FIG. 10. Vertical cross section of the thallus of *Marchantia*.

Sometimes on the dorsal surface the plant possesses cup shaped structures called gemma cups (Fig. 9, B). These cups contain special

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structures meant for vegetative reproduction, which are known as **gemmae**.

The thallus in a vertical cross section exhibits a clear differentiation of tissues. On the upper side there is a clear single layered epidermis called the upper epidermis It is thin walled and possesses chloroplast. It is not continuous but is broken at various places by barrel shaped cells, which form air pores. The latter look like stomata of the plants of higher groups, but they are quite different from them as they cannot change their size. That is the opening of the pore neither increases nor decreases. The pores communicate into the assimilatory chambers. Each assimilatory chamber consists of simple or branched filaments, which originate from its base (Fig. 10).

The chambers are separated from each other by means of partition walls which are two to four cells in height. The cells of the filaments possess chloroplasts and thus form the assimilatory tissue. Just beneath it is the major portion of the thallus, which is made up of ordinary thin walled parenchymatous cells containing starch. This part of the thallus constitutes the storage region. A few of its cells may possess oil and mucilage.

The lower side of the thallus also possesses a single layered epidermis which is called the lower epidermis. It possesses smooth walled and

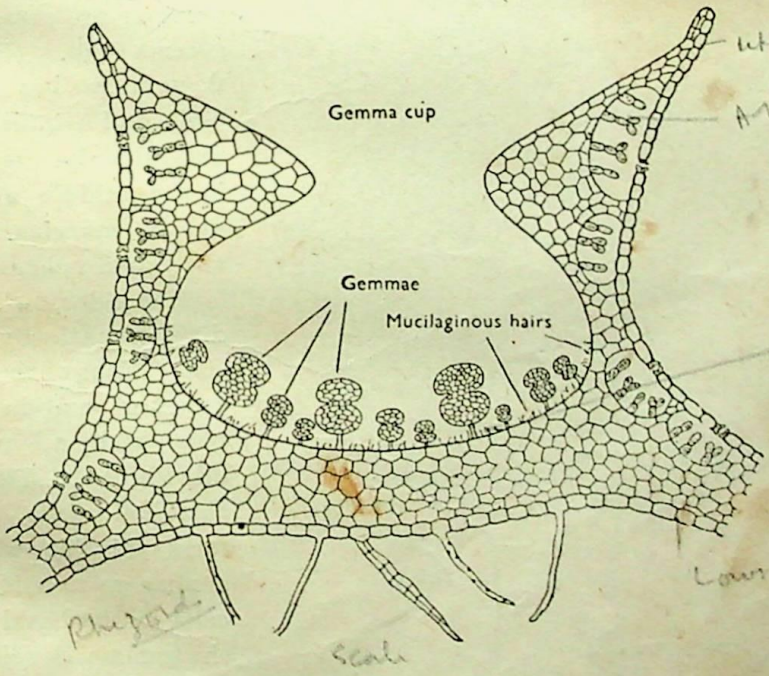

FIG. 11. Section of the *Marchantia* thallus passing through a gemma cup showing many gemmae and mucilaginous hairs.

tuberculate rhizoids. Besides these a number of scales are also present on this side of the thallus.

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Reproduction. *Marchantia* reproduces by two methods.

1. *Vegetative.*
2. *Sexual.*

1. **Vegetative.** It takes place in a variety of ways.

(a) By progressive death and decay of the older parts reaching dichotomy. At this place the individual branches become separate and each branch gives rise to a new plant.

(b) Some species grow by means of adventitious branches which are developed on the ventral surface of the thallus. These branches, when separated, form a new plant

(c) A more common and special method of vegetative reproduction in this genus is by means of gemmae, which are produced in gemma cups These cupules develop on the dorsal surface of the thallus slightly away from the growing point. In the beginning these are circular but later on form hollow cavities on account of the development of neighbouring vegetative tissue. Many gemmae are present in a gemma cup. (Fig. 11). A gemma has a small stalk and a multicellular discoid body. It is thick in the middle and thin at the margins. There are two notches on the lateral sides, which are diagrammatically opposite. Most of the cells of a gemma contain chloroplast, while a few possess oil (Fig. 12). There are rhizoidal cells, which form rhizoids when the gemma germinates. Some cells on the basal side of the gemma develop into club shaped hairs. These hairs secrete mucilage which absorbs water. It causes the gemma to break from the cupule. Each gemma on germination gives rise to two new thalli.

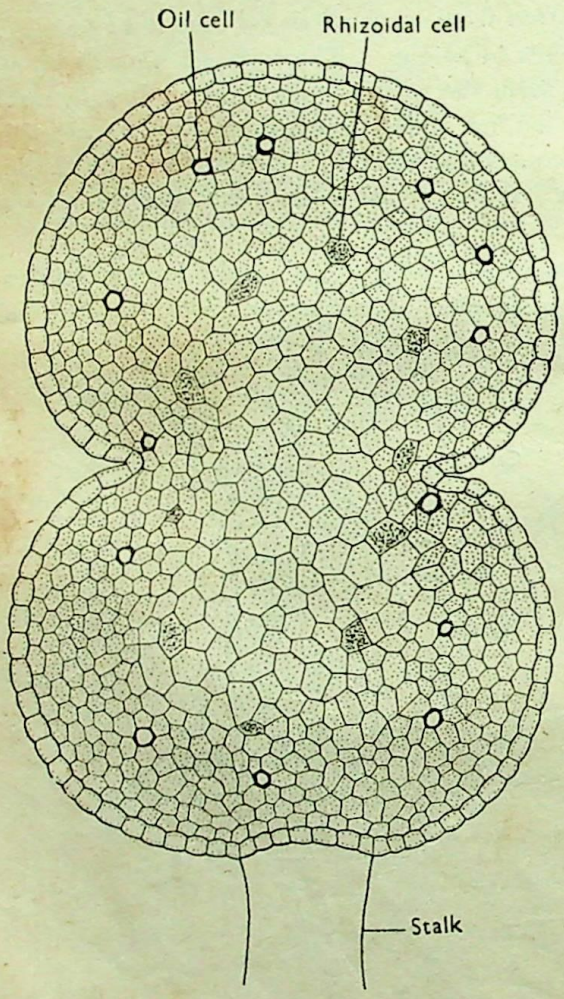

FIG. 12. A single gemma with a small stalk.

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Sexual. It takes place with the help of male and female organs of reproduction called **antheridia** and **archegonia**. Both these organs are borne on special branches called **antheridiophores** and **archegoniophores** respectively. The plants are dioecious and so antheridiophores and archegoniophores are developed strictly on different thalli.

The gametophores have a long stalk at the end of which are present horizontal disc like structures. In fact these sexual branches are nothing but the continuation of the mid-rib of their respective thalli.

Antheridiophore and antheridia. As stated already, the male branch or antheridiophore (Fig. 9, C) is a modified branch of the thallus. It has

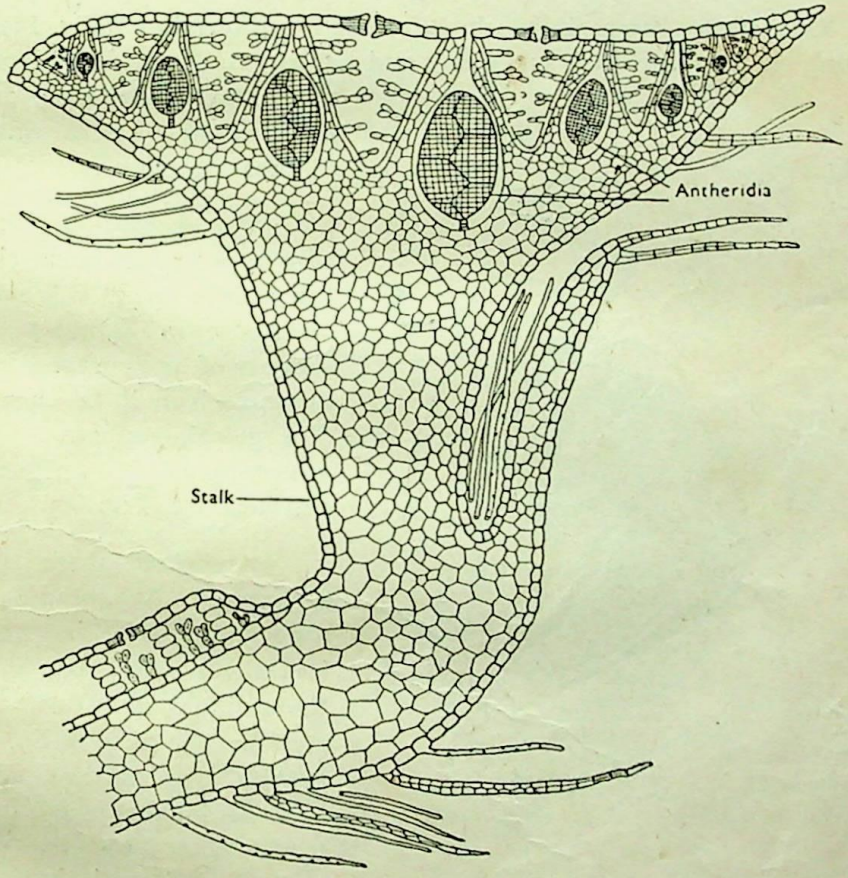

FIG. 13. Section of the antheridiophore of *Marchantia* showing the arrangement of male organs, the antheridia.

a short stalk with an eight lobed flat peltate disc at its apex. The eight lobed condition of the disc is due to the repeated forking of the young

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branch. As a result of these divisions very often eight lobes are formed though occasionally their number may be reduced to four in certain species. The stalk has two grooves on the side from where rhizoids and scales are given out and this side corresponds to the ventral side of the thallus.

The peltate disc is slightly convex. In a vertical section it exhibits the same structure as the thallus, of which it is a modified branch. On the upper side there is a single layered epidermis which has many barrel shaped pores. Each pore opens into a photosynthetic chamber. Alternating with these pores are other openings which lead into big antheridial cavities (Fig. 13).

Each cavity has a single short stalked antheridium (Fig. 14). On ripening each antheridium has many androcytes. In its mode of development it exhibits more or less the same stages as the antheridium of *Riccia*.

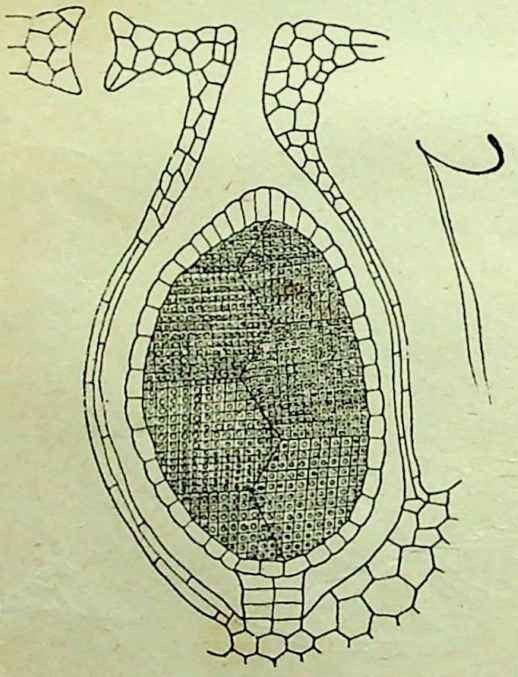

FIG. 14. Single antheridium in a cavity. Lying outside is an antherozoid.

The absorption of moisture by a mature antheridium causes it to open. According to Anderson (1931) large number of spermatozoids are liberated from it in the form of a gelatinous mass. Each spermatozoid is uninucleate and biciliate (Fig. 14).

Archegoniophore and archegonia. As already stated archegoniophore is nothing but the upward bending of the ordinary prostrate vegetative branch (Fig. 9, D). The branch like nature of the archegoniophore is further made clear by its dorsoventral differentiation. The side which corresponds to ventral region has two longitudinal furrows, each possessing rhizoids and scales while the other corresponding to dorsal region has air chambers.

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capsule is mature there is a sudden increase in their size. This facilitates the capsule to come out by rupturing the protective sheaths (Fig. 18, B).

In the epibasal region, which forms capsule, periclinal walls are laid down thus differentiating the outer **amphithecium** and an inner **endothecium**. The former forms the jacket layer, while the latter forms the **archesporium**. The cells of the archesporium divide again and again and give rise to sporogenous tissue. Sooner or later the cells of this tissue also divide. Half of these give rise to **spore mother cells** (Fig. 18, D) while half turn out sterile. The latter merely elongate and form **elaters** (Fig. 18, A, C,). In most of the species spore mother cells and elaters are evenly distributed within the capsule. Sooner or later each spore mother cell divides twice tetrahedrally, (Fig. 18, E), first being a reduction division, to give rise to four haploid spores (Fig. 18, F). The elaters are hygroscopic in nature and by their activity bring about the liberation of the spores after the dehiscence of the capsule.

Thus at maturity the sporogonium is differentiated into a massive foot, an elongated seta and a spherical capsule containing many spores (Fig. 18, B).

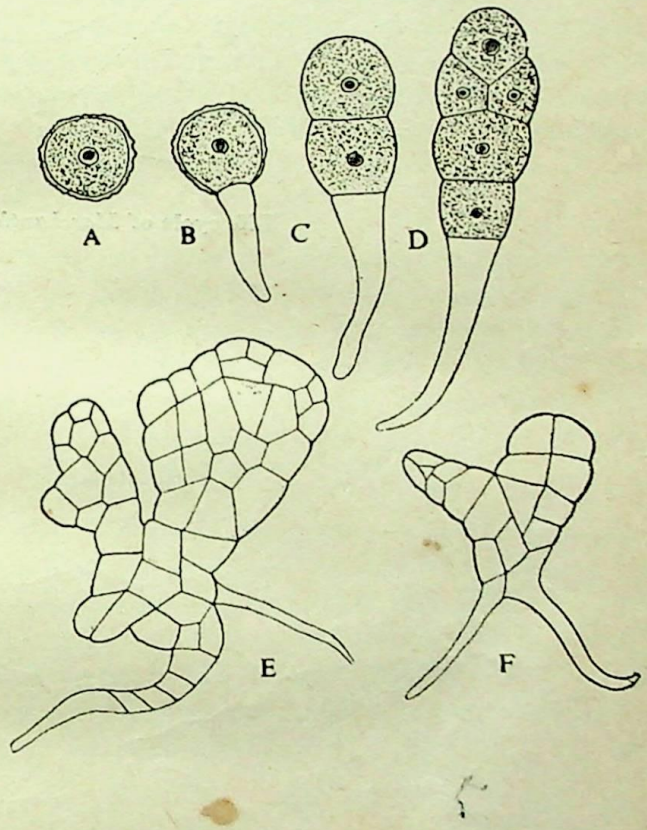

FIG. 19. A—F, stages in the germination of the spore of *Marchantia* and formation of a new thallus.

Structure and germination of the spore. Each spore is uninucleate and possesses two walls, an outer **exosporium** and an inner **endosporium** (Fig. 19, A). The spores start their germination as soon as they reach a suitable place. Each spore sends out a small filamentous outgrowth (Fig. 19, B). This tiny structure ultimately develops into

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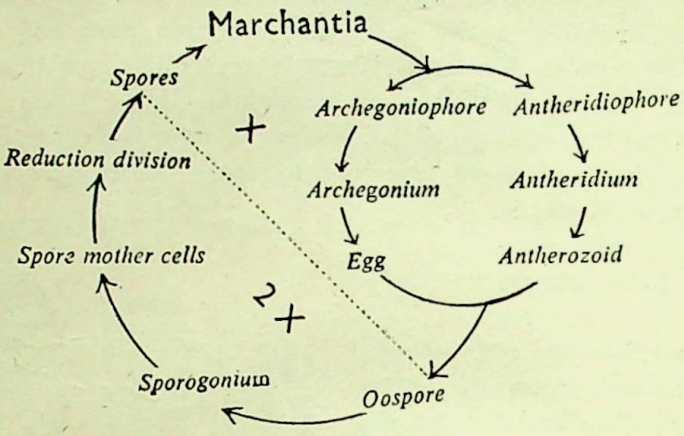
a new thallus (Fig. 19, C—F). The spores may remain viable even after a year. The new thallus of **Marchantia** is thus heteroblastic in development, *i. e.*, it arises indirectly through an independent structure, the protonema.



Life cycle of *Marchantia*.

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CHAPTER 3

ANTHOCEROTAE

This group differs from *Hepaticae* in so many respects that it has become absolutely essential to give it an entirely different position. It has been given a place intermediate between *Hepaticae* and *Musci* and therefore morphologically this group occupies an important position. It is a small group of plants contaning hardly six genera. They are all closely allied in the structure of their gametophyte and sporophyte and are placed in a single family *Anthocerotaceae* within a single order *Anthocerotales*.

All the members are characterised by the presence of a simple dorsoventrally differentiated lobed thallus with or without a definite mid-rib. In most of the species the cells which constitute the thallose structure contain a single chloroplast with a prominent **pyrenoid**. There is no internal differentiation of tissues and only smooth walled rhizoids are present on the ventral side. Scales are entirely lacking. *Nostoc* colonies are present in the tissue of the gametophyte.

The sex organs are embedded on the dorsal side of the plant body. Antheridia are endogenous in their development and are situated in groups. Archegonia are sunken. Another important feature is the presence of a highly developed sporophyte with a bulbous foot and a very prominent capsule. The sporogonium is meristematic on account of the presence of an active intercalary meristem. Sporogenous tissue in the capsule is derived from amphithecium.

Systematic position.

Bryophyta.
Anthocerotae.
Anthocerotales.
Anthocerotaceae.
Anthoceros.

Occurrence. It is cosmopolitan in distribution, but avoids dry-places. It is found in moist and shady places. It may also be seen in the hollows of moist rocks, on the sides of ditches and at other wet places. The thalli of *Anthoceros* are confined to hills and various

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other cold places. Kashyap has reported five species from Western Himalayas. They are ; *A. erectus, A. himalayensis, A. chambensis, A. gollani* and *A. longii*. Sane (1942) reported two species of *Anthoceros* from India. They are *A. dixiti* from Lonavola and *A. sahyadrensis* from Poona. Pande and Ahmad reported *A. crispulus* from Lucknow (1943). Nearly half a dozen species are found in Britain.

Structure. The dark green dorsoventrally differentiated thalli of *Anthoceros* are transluscent. The dark green colour is due to the presence of *Nostoc* colonies which form blue green masses inside the thallus and which may be visible to the naked eye. The thallus is narrowly or broadly lobed and has crenate margin. Mid-rib may or may not be distinct (Fig. 20).

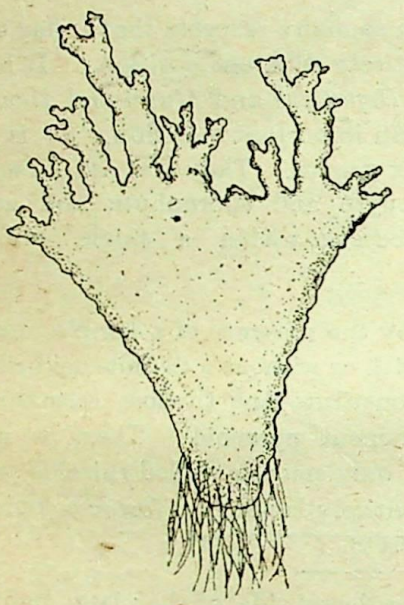

FIG. 20. Habit of *Anthoceros*.

Internally the structure of the thallus is very simple. It is made up of parenchymatous cells while upper and lower surfaces are composed of smaller cells and constitute upper and lower epidermis. Each cell has one chloroplast containing a single pyrenoid. According to McAllister (1914, 1927) the pyrenoids here are quite different from the pyrenoids of *Chlorophyceae*. On the ventral side of the thallus there are some intercellular cavities which open to the out side by slime pores. These cavities very often contain a *Cyanophycean* alga, the *Nostoc*. The presence of the alga may not be regarded as a case of symbiosis as it has definitely been shown by Pierce (1906) that the presence of the endophytic alga has nothing to do with the growth of the thallus. In some species, according to Proskauer (1951), these cavities may be completely absent. It may, therefore, be presumed to be a case of mere space parasitism. Smooth walled rhizoids, which fasten the thallus to the ground are also present on this side. Scales and mucilaginous hairs are absent (Fig. 21).

Reproduction. It is brought about by two methods.

1. *Vegetative.*
2. *Sexual.*

1. Vegetative. It takes place in a variety of ways.

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A. Vegetative propagation is brought about by the progressive growth of the apical portion and subsequent death of the posterior region of the thallus.

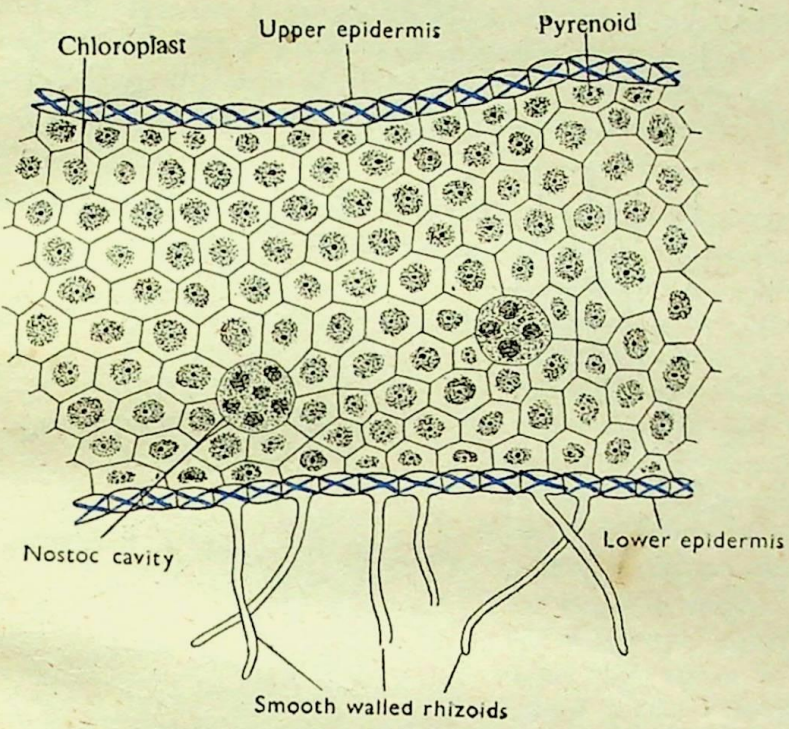

FIG. 21. Vertical cross section of the thallus of *Anthoceros*

B. Sometimes **tubers** are formed during unfavourable circumstances. Their position varies in different species. They also help the plant to tide over unfavourable periods and bring about vegetative multiplication.

C. In certain species of *Anthoceros* the whole plant dies out during unfavourable conditions except the growing point. On the return of favourable conditions this portion gives rise to the new plant as in *A. pearsoni*.

D. In case of *A. glandulosus*, different types of vegetative bodies are produced which are called the **gammae**. They are developed on the upper side of the thallus and they also form new plants.

Sexual. The thalli of *Anthoceros* may be monoecious (*A. himalayensis*) or dioecious (*A. halli*). The former is protandrous. The male and female organs of reproduction, antheridia and archegonia are embedded in the tissue of the thallus. Sometimes the antheridia are visible to the

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naked eye if the thallus is seen against light, but the archegonia are not

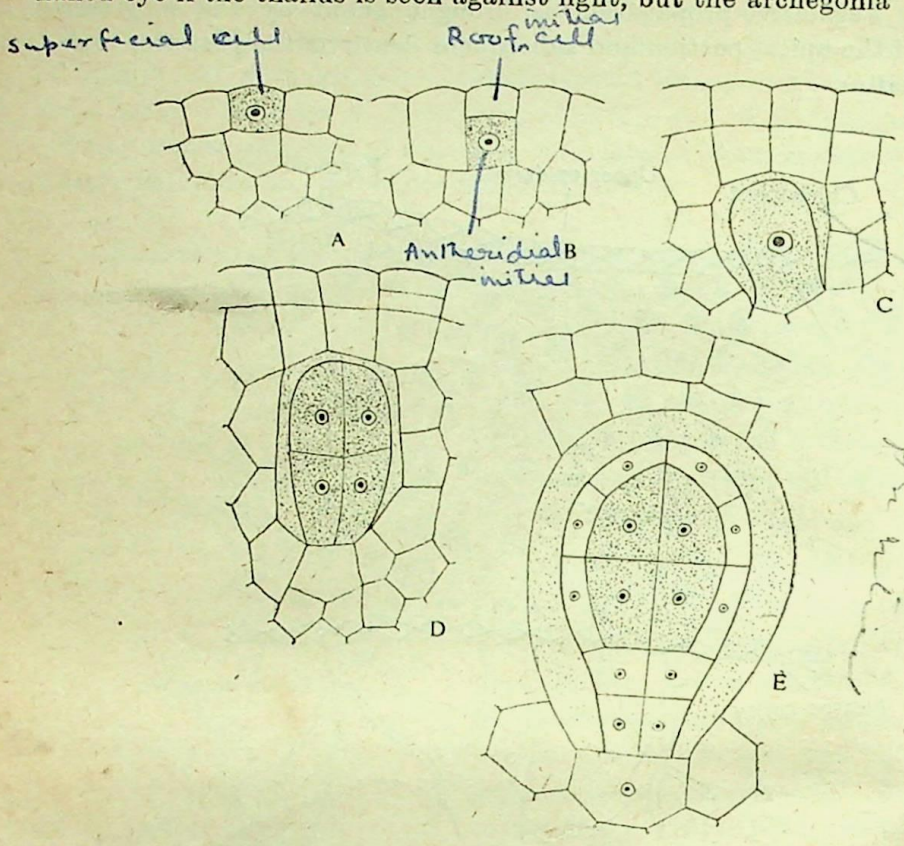

FIG. 22. Stages in the development of the antheridia of *Anthoceros*. A, superficial cell. B, transverse division of the superficial cell. C, mucilage filled space between roof initial and antheridium initial. D, divisions in the antheridium initial. E, formation of jacket cells and primary androgonial cells.

easily detectable as these are deeply sunken. They can be seen only in a vertical cross section of the thallus.

Development and structure of antheridia. They are produced in groups and their development, as already stated, is **endogenous**. No doubt they develop on the upper surface of the thallus but the cavities in which they develop do not open to the outside.

The development of a single antheridium starts with a **superficial cell** (Fig. 22, A) of the thallus which lies near the growing point. The superficial cell divides periclinally into an **outer cell** and an **inner cell** (Fig. 22, B). According to Campbell and Haupt, the division in the superficial cell is transverse. Anyhow, two cells so formed are called **antheridial initial** (lower one) and **roof initial** (upper one). Between these two cells a mucilaginous cavity appears which later on enlarges and forms an antheridial chamber (Fig. 22, C). As the name indicates, roof

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initial divides again and again by anticlinal and periclinal divisions and ultimately forms a roof above the antheridial initial. The roof is two cells thick. The antheridium initial gives rise to an antheridium or a number of antheridia as the case may be. In the latter case the initial divides vertically into two to form cells, each of which gives rise to a single antheridium. Thus antheridial chamber may contain two to four antheridia. According to Mehra and Handoo (1953) more than four antheridia may be present in an antheridial cavity as in the case of *A. erectus*.

The antheridium initial divides first by a vertical wall and then by another wall at right angles to the first (Fig. 22, D). A transverse wall is again laid down with the result that two tiers of four cells each are formed. The lower tier divides by transverse wall and forms the stalk of the antheridium. The upper tier further divides by a transverse wall resulting in the formation of an octant. Sooner or later periclinal divisions take place in the octant so that a peripheral jacket of eight sterile cells is formed, which surrounds a mass of eight androgonial cells (Fig. 22, E). The latter by repeated divisions give rise to androgonial cells. According to Bagchee (1924) rest of the stages of spermatogenesis are more or less the same as have been described in the life histories of other bryophytes. Ultimately an androcyte, formed by an androcyte mother cell, gets metamorphised into an uninucleate and biflagellate antherozoid.

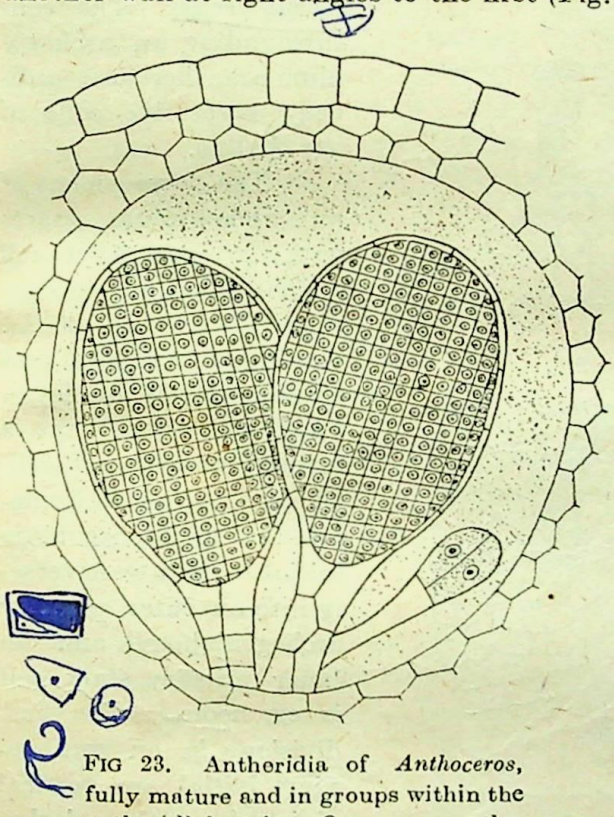

FIG 23. Antheridia of *Anthoceros*, fully mature and in groups within the antheridial cavity. One young antheridium is also seen,

Thus each antheridium, at maturity, is more or less a club shaped structure with a short stalk. The single layered peripheral cells form the outer jacket inside which there is a large number of antherozoids (Fig. 23). At maturity the roof of the antheridia ruptures and thus

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they become exposed to the outside. Later on they absorb water and burst thus liberating the antherozoids.

Development and structure of archegonia. The archegonia of *Anthocerotales* are embedded in the tissue of the thallus and are developed separately. Neck and venter of the archegonia are in direct contact with the thallus and, therefore, they do not remain surrounded by a jacket of sterile cells. The cells surrounding an archegonium are, therefore, ordinary vegetative cells of the thallus.

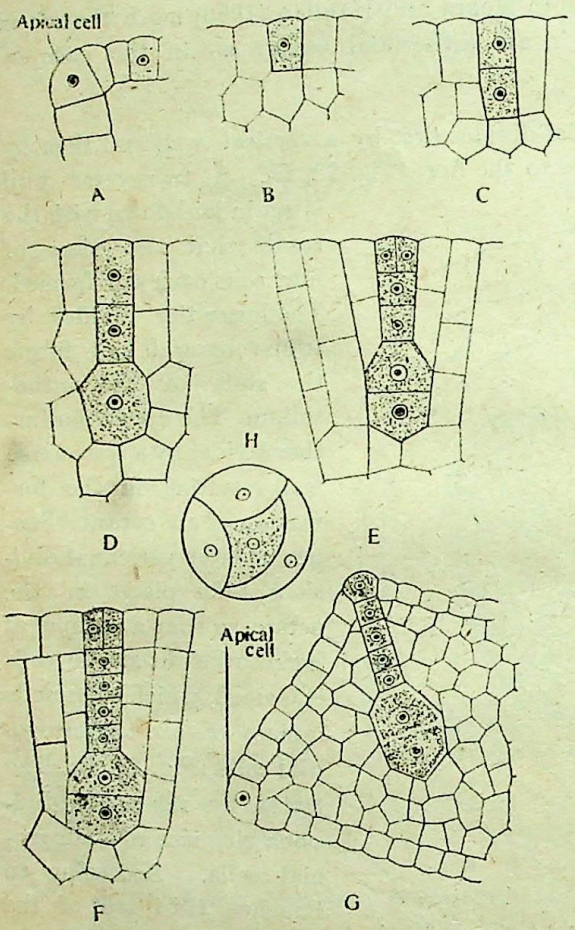

FIG 24. Stages in the development of the archegonia of *Anthoceros*. A, archegonial initial in relation to apical cell. B, archegonial initial. C, transverse division. D, cover initial, primary neck canal cell and primary ventral cell. E-G, fully mature archegonium.

The development of an archegonium starts with a **superficial cell** which acts as an archegonium initial (Fig. 24, A). According to Mehra and Handoo (1953) the latter functions directly as a primary archegonial cell. The earlier view of Campbell that an archegonium initial divides transversely into an outer primary archegonial cell and an inner primary stalk cell is erroneous. The first divisions in an archegonium initial are vertical giving rise to three **jacket initials**, surrounding an axial cell (Fig. 24, B, H). The latter divides transversely into a cover initial and a central cell (Fig. 24, C). The cover initial divides vertically only once or twice to give rise to two or four cover cells, while the central cell divides transversely forming a primary **neck canal cell** and a **primary ventral canal cell** (Fig. 24, D). Now the former divides transversely giving rise to a neck of four to six or even more cells arranged vertically. The ventral canal

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The capsules arise from the thallus and when fully mature, look like a small grass or bristle and are two or three inches in length. Each capsule exhibits the following structures. At the base there is a bulbous **foot** which consists of parenchymatous cells but palisade like cells may also be there. The space between foot and capsule is occupied by some **meristematic cells** which go on adding to the length of the capsule even when it is completely mature. A capsule has **columella** in the middle while the outermost layer is epidermis. The latter possesses stomata at many (Fig. 26) places, which are similar to the stomata of the higher plants. So in this respect the sporophyte is very much advanced. Moreover, if the foot deepens slightly more into the soil just to get all the water supply and mineral nutrients, it may become absolutely independent. Also it can maintain itself for quite a long time without any help from the gametophyte though according to Rink (1935), the sporophyte cannot develop fully without the food supply from the gametophyte. Even then it is highly advanced.

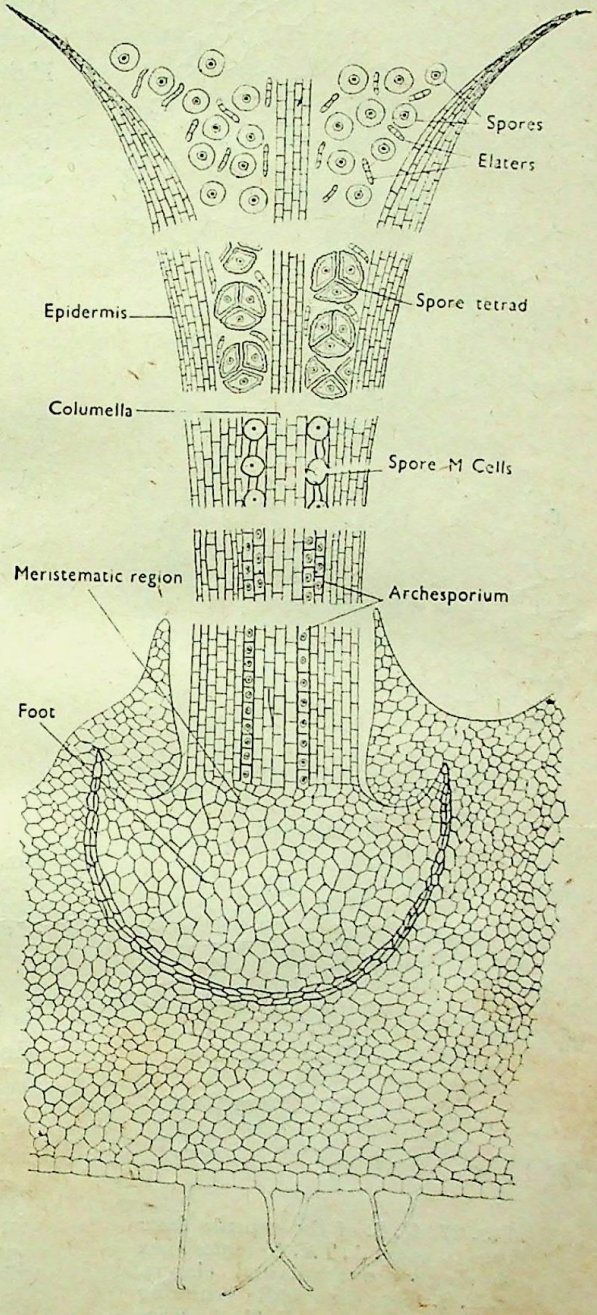

FIG. 26. L. S. of the *Anthoceros* capsule showing different regions from base to apex. The capsule is embedded in the thallus.

The capsule possesses the sporogenous mass, the **archesporium**, which is derived from

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the amphithecium, as already stated. Different stages of the archesporium may be seen at the different levels of the capsule. Near the foot is the archesporium which is single layered, though it becomes double layered at a slightly higher level. Above it are the spore mother cells, which at the top divide into tetrads and finally give rise to spores (Fig. 26. 27, A, B, C).

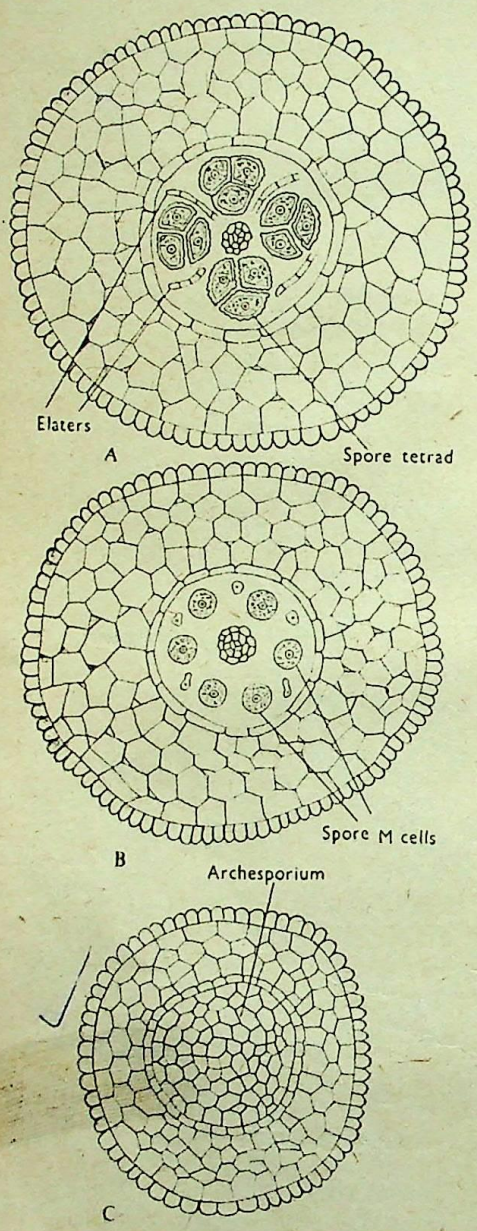

FIG. 27. T. S. of the capsule from base to apex. A, T.S. from the apex showing spore tetrads and elaters. B, T. S. from the middle showing spore mother cells. C, T. S. from the base region showing archesporium in the middle.

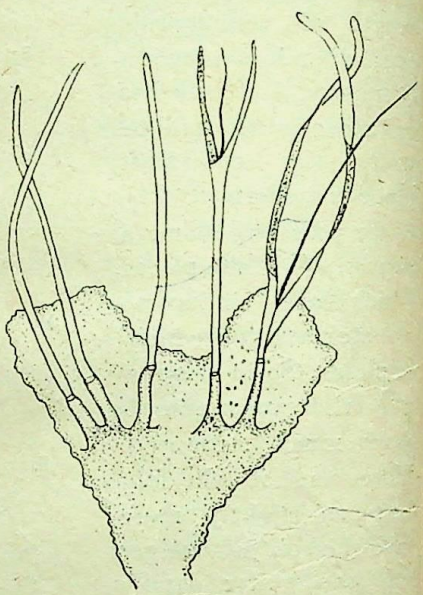

FIG. 28. *Anthoceros* gametophyte with sporophytes. Some of the sporophytes show the manner of dehiscence.

The capsule when dried, is brown or black in colour. It finally dehisces, the dehiscence being dependent on the loss of water. The hygroscopic movement of the pseudoelaters, epidermis and other layers help in the dispersal of the spores (Fig. 28).

Structure and germination of spores. Each spore is uninucleate and possesses two walls. The outer one is called **exine** while the inner one is known as

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intine (Fig. 29, B). It has a single colourless plastid, oil globules and food material. It germinates either directly or may rest for some-time before the actual germination. Whenever it germinates, the exine ruptures and the intine comes outside in the form of a tube called a germinal tube or **protonema.** The latter turns green and its terminal cell acts as apical cell (Fig. 29, C). It cuts off segments and forms a new thallus (Fig. 29, D). Most of the species are homothallic, but according to Proskauer (1948) some species may be hete-

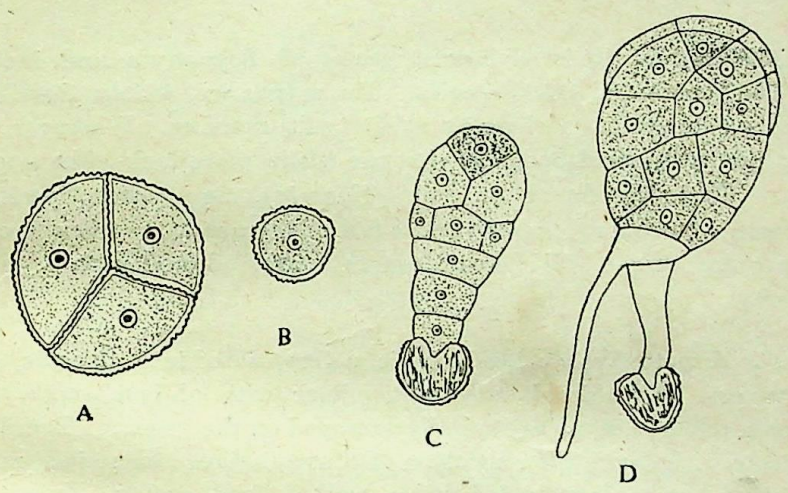
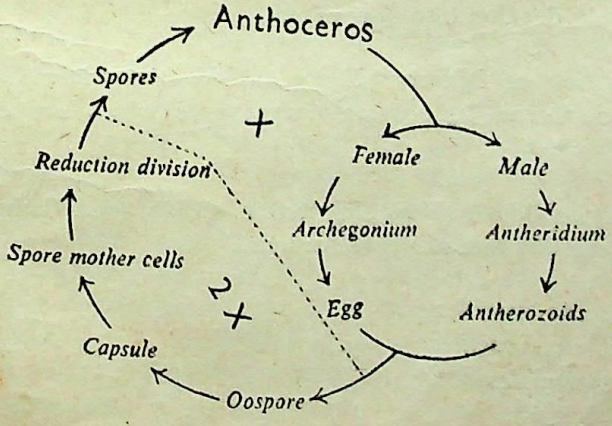


FIG. 29. Germination of the spore of *Anthoceros* and the formation of a new thallus.

rothallic. In the latter species determination of sex is **genotypic**. Out of the four spores of a tetrad two develop into male gametophytes while the other two give rise to female gametophytes.



Life cycle of *Anthoceros*.

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CHAPTER 4

MUSCI

Introduction. It is the largest group of Bryophyta and includes about 660 genera and 14500 species. The mosses are widely distributed and occur perhaps everywhere except in salt marshes. Wherever they grow, they thrive so abundantly that the whole place looks like a green valvet. They are found on soil *(Funaria)*, in water (Species of *Sphagnum)*, on rocks *(Andrea)* and a few of them may be seen growing on decaying wood *(Weberea nutans)* and decaying tree trunks *(Mnium)*.

The gametophytic plant body is differentiated into rhizoids, stem and leaves. The rhizoids are multicellular with oblique septa, while the green papery leaves are spirally arranged on the stem. The latter is delicate with slight differentiation of tissues inside. There is a middle conducting region surrounded by a well defined cortex. Xylem and phloem, however, are always lacking. The plants, at maturity, bear sex organs which are developed from the superficial cells of the gametophyte.

Fertilization ends the gametophyte generation and the sporophyte which is formed is generally differentiated into foot, seta and capsule. The latter produces only spores which on germination give rise to a branched structure. It is on these structures that protonema are borne which ultimately develop into new plants.

Classification of Musci. Many classifications have been put forward from time to time by different bryologists which are enumerated below.

According to Bower (1935), Wettstein (1935) and Campbell (1928, 1940) *Mosses* are divided into three orders.

1. *Sphagnales*
2. *Andreaeales*
3. *Bryales*

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Dixon (1932) slightly modified the above classification. He gave these three orders a status of a sub-class. So according to him the *Mosses* are divided as follows.

Class. **MUSCI**
Sub-class 1. **Sphagnales.**
Sub-class 2. **Andreaeales.**
Sub-class 3. **Bryales.**

Smith (1935, 1955) divided the class *Musci* into three sub-classes.

Sub-class 1. **Sphagnobrya.**
Sub-class 2. **Andreaeobrya.**
Sub-class 3. **Eubrya.**

According to Engler, Werdermann and Melchior (1954) the *Musci* have been divided into five sub-classes.

Sub-class 1. **Sphagnidae.**
Sub-class 2. **Andreaeidae.**
Sub-class 3. **Bryidae.**
Sub-class 4. **Buxbaumiidae.**
Sub-class 5. **Polytrichidae.**

Parihar (1956) has divided *Musci* into three sub-classes.

Sub-class 1. **Sphagnidae.**
Sub-class 2. **Andreacidae.**
Sub-class 3. **Bryidae.**

The classification of Smith has been followed in this chapter.

SPHAGNOBRYA

The sub-class is characterized by the presence of thallose protonema which is usually one cell thick. The leaves in the gametophyte are conspicuous by the absence of a mid-rib. It differs from rest of the *Musci* in the development of its sex organs. It is regarded as the most primitive sub-class of *Musci*. A very important feature is that the sporogenous tissues of the sporophyte develops from the amphithecium. The sporophyte possesses a very small seta. In fact it is elevated by the growth of a stalk developed from the gametophytic tissues called pseudopodium. Thus seta has no function to perform so far as the elevation of the sporophyte is concerned The capsule has a cap like structure called the operculum while peristome is wanting. Columella is developed from the entire endothecium.

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The sub-class has a single order *Sphagnales* which includes a single family *Sphagnaceae*. The family is monotypic, that is, it has only one genus—*Sphagnum*.

Systematic position

Sphagnobrya.
Musci.
Sphagnales.
Sphagnaceae.
Sphagnum.

Occurrence. The genus includes about 335 species. Its distribution is world wide and extends from tropics to temprate regions except the

FIG. 30. Habit of *Sphagnum*. A, a fully mature gametophyte. B, a portion of stem and leaves magnified.

arctic zone. It is calcifuge. It is mostly found in swampy places, in pools, on the banks of lakes and on wet rocks of hills. Sometimes it covers the whole surface of the lake near which it is growing and forms the quaking bog. Under such conditions some angiosperms may also be

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associated with it. Some acid is given by the plant which retards the decay of the dead tissue. Thus the dead and decaying mass of plants accumulates year after year. This compact mass when hardens is called a **peat**. It is therefore also called a peat moss. From ecological point of view it is a very important factor. The colour of the plant is pale green but it may be red or yellow. The colour of the dry plants is dull. Plants absorb and retain water like a sponge. Nearly a dozen species have been reported from this country.

Structure. The plants of *Sphagnum* are fairly large in size The aquatic forms may be several feet in length. The young plants are differentiated into rhizoids, stems and leaves. Rhizoids, however, disappear as the plants mature. The stem is very much branched and continues to grow indefinitely (Fig. 30, A). Normally the branching is lateral. These structures may be discussed separately.

Rhizoids. As already stated, they are present only in the earlier stages and disappear as the plant matures. They are delicate and colourless structures with oblique septa.

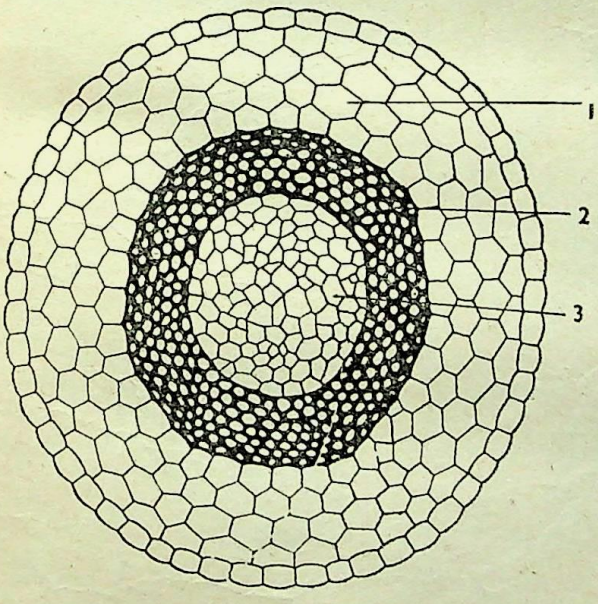

FIG. 31. T.S. of the stem of *Sphagnum*. 1, Cortex. 2, outer thick walled prosenchymatous region. 3, axial cylinder.

Stem. The size of the stem varies according to the species. As described earlier, it is very much branched and branching is normally lateral. In aquatic species the branches spread out from the tsem and are all similar. In rest of the species branches are of two types–the drooping and the elongated branches which are loosely arranged round the stem and others are the divergent type of branches which are short and grow upwards.

In a transverse section the stem shows a clear differentiation of tissues (Fig. 31). Outermost layer is cortex or **hyalodermis** which may

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be five to six cells in thickness. In the beginning it is always single layered but becomes many layered later on. In lateral branches it is always one cell thick. It takes part actively in the absorption of water by capillary action, as rhizoids are no more present in mature plants.

The middle layer consists of thick walled prosenchyma or **hadrome,** while the inner most layer is called **medulla.** The latter is thin walled having colourless cells with collenchymatous thickenings. It corresponds

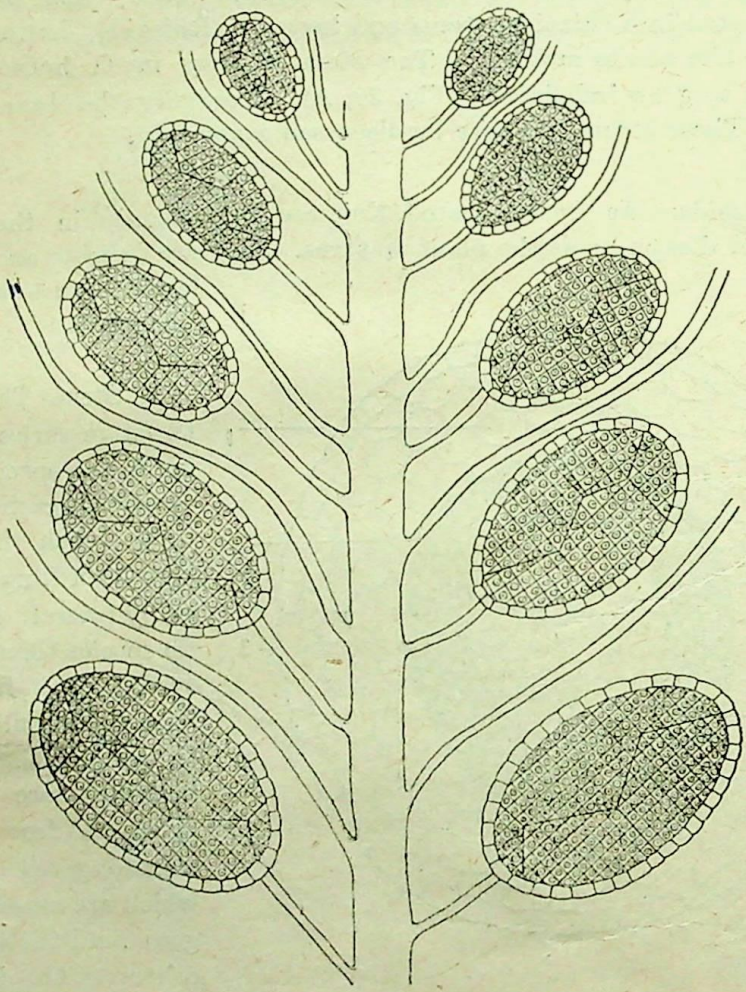

FIG. 32. L. S. of an antheridial branch showing the acropetal arrangement of antheridia and leaves.

to the pith of higher plants. No well defined conducting region is present in case of *Sphagnum*.

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Leaves. As mentioned above, they are spirally arranged on the stem. They are thin and small. They are invariably green on the sterile branches but on the fertile branches their colour becomes dark green, red or yellow. A leaf blade consists of two types of cells—narrow living assimilatory cells containing chlorophyll and big dead, empty hyaline cells having open pores. The latter absorb water as there is no mid-rib in the leaf (Fig. 30, B). The arrangement of cells in a mature leaf is reticulate.

Reproduction. It takes place by two methods.

1. *Vegetative.*
2. *Sexual.*

1. **Vegetative.** Any branch within a tuft may grow upwards. When it reaches the height of the main axis it breaks away owing to the death of the axis bearing it. The portion so broken and separated functions as a new independent plant.

2. **Sexual.** The plants of *Sphagnum* may be monoecious or dioecious Even in case of monoecious species sex organs occur on different branches. The reproduction takes place with the help of male and female

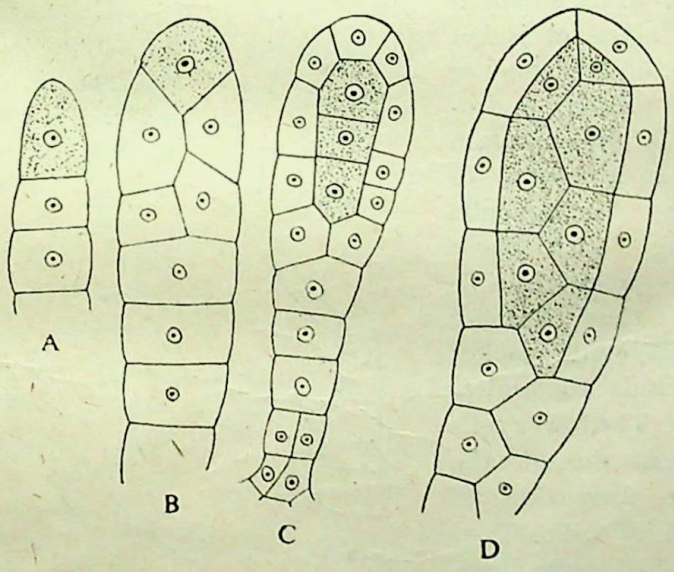

FIG. 33. Stages in the development of the antheridium of *Sphagnum*.

reproductive organs called **antheridia** and **archegonia** respectively. The sex organs develop on short lateral branches near the apex of a plant.

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Development and structure of antheridium. A male branch appears like a small catkin and is characterized by the presence of brightly coloured leaves. The colour, however, may vary. A single antheridium is situated in the axil of a leaf and therefore it is axillary in position, or in other words, antheridia occupy the place of a lateral vegetative branch. They are produced in acropetal succession (Fig. 32).

A superficial cell of the stem acts as an **antheridium initial.** Now transverse divisions follow in quick succession resulting in the formation of a filamentous structure (Fig. 33, A). As the filament continues its growth its terminal cell acts as an apical initial with two cutting faces (Fig. 33, B). The division continues till it becomes 12-15 cells in height. At this stage there are two successive vertical divisions in the last 2-5 segments cut off from the apical cell. The first division cuts a jacket initial and a large sister cell (Fig. 33, C). The second division cuts off the latter cell into **jacket initial** and a primary **androgonial cell.** The antheridium now consists nearly 2-5 primary androgonial cells surrounded by a layer of jacket initials (Fig. 33 D). Sooner or later the primary androgonial initials divide again and again to give rise to innumerable **androgonial cells** Along with these changes the jacket initials also divide thus forming a single layered jacket which surrounds the androgonial cells. The lower cells of the filament do not take part in the formation of the androgonial cells. They simply divide longitudinally and transversely to give rise to a long stalk which is two cells broad (Fig. 34, A).

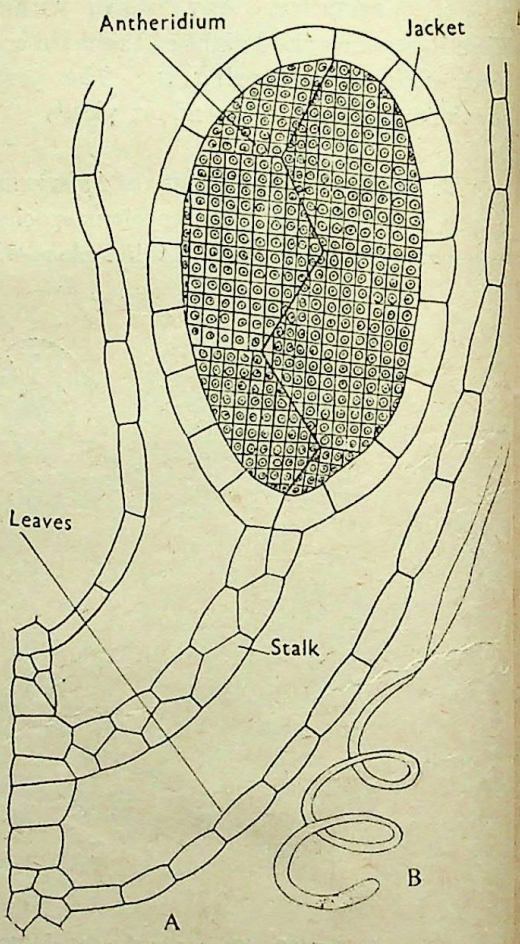

FIG. 34. A fully mature antheridium of *Sphagnum*

The antherozoids which are formed inside the antheridium are uninucleate and biflagellate (Fig. 34, B). According to Muhldorf (1930)

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in their structure they are similar to the antherozoids of *Hepaticae*. At maturity the antheridium absorbs water and gets open from the apex thus liberating a large number of antherozoids.

Development and structure of archegonium. Archegonia are produced on the archegonial branches which are short. The leaves of these branches are bright green in colour and big in size. The number of archegonia on each branch varies from one to five but usually only three are present. One of them is a primary archegonium while others are secondary. The initial stages of development of all the archegonia are similar.

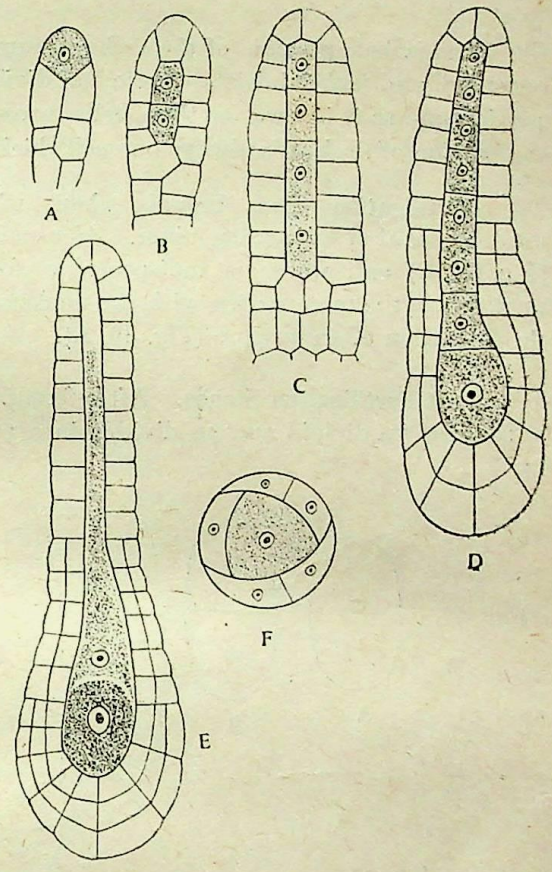

FIG. 35. Stages in the development of the archegonium of *Sphagnun*. A, apical cell. B, C, transverso divisions. D, fully mature archegonium. E, archegonium ready for fertilization. F. T. S. of the archegonium.

First a small filament, hardly 4-5 cells in height, is produced. In case of primary archegonium it is formed either by the successive transverse divsion of the terminal cell or the latter acts as an apical cell (Fig. 35, A) with two cutting faces During the formation of secondary archegonia apical cell is never differentiated. When the filament is 4-6 cells in length vertical divisions take place in the terminal cell cutting three jacket initials and a single axial cell. Now the latter divides transversely to give rise to a cover initial and a central cell (Fig. 35. B). By a further transverse division the central cell divides into a primary neck canal cell and a primary ventral canal cell (Fig. 35, C). The former by successive

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transverse divisions gives rise to a neck of 8-9 cells in height while the latter divides transversely only once forming a ventral canal cell and an egg (Fig. 35, D). According to Bryan (1915)and Melin (1916) both these cells are of nearly equal size.

The jacket portion of the archegonium is formed from the primary cover cell and jacket initials. Periclinal divisions take place in the venter portion and so it is two or three cells broad in this region, while in the portion of neck it is always one cell thick.

Fertilization. It is brought about when many antherozoids pass into the canal of the archegonium. As usual neck canal cells disorganise (Fig. 35, E) and water is indispensable for fertilization Finally the nucleus of the male unites with the nucleus of the female resulting in the formation of an oospore (Fig. 36, A).

Post Fertilization Stages. After fertilization the oospore increases in size and its diploid nucleus divides into two by a transverse division

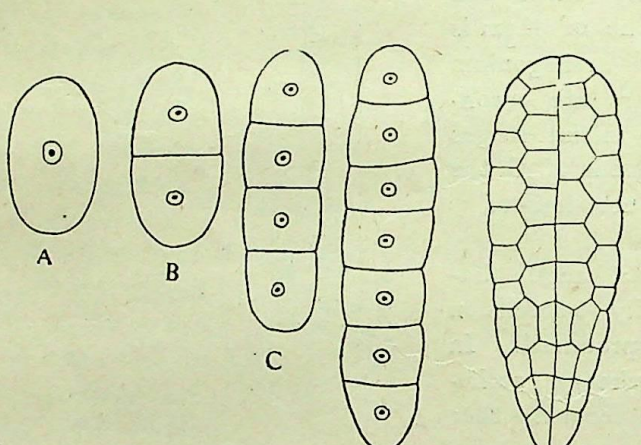

FIG. 36. Stages in the development of the sporophyte of *Sphagnum*.

(Fig. 36, B). According to Bryan* (1920) more transverse divisions follow resulting in the formation of 5—12 celled embryo (Fig. 36, C). The upper half of the filamentous embryo gives rise to the capsule, middle portion develops into foot and seta while the lowermost region forms a haustorium (Fig. 36, E). Each cell of the upper half divides twice vertically. Thus quadrants are formed. Periclinal divisions are now laid down differentiating amphithecium and endothecium. The latter divides again and again and gives rise to a central sterile tissue called **columella**. Amphithecium also divides by periclinal

* Bryan (1920) reported gametic union of ventral canal cell and egg.

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divisions. It results in the formation of an outer sterile layer and an inner fertile layer, the **archesporium**. The latter forms a semicircular arch over columella and forms the **sporogenous tissue** which is two to four cells in thickness. Sporogenous cells are present inside it. According to Melin (1915) each cell undergoes the normal meiosis and gives rise to four spores. So a very large number of spores are present inside the spore sac.

The wall of the capsule which is 3—7 layers thick is formed by the cells of the outer sterile tissue derived from the amphithecium. The outermost layer forms the epidermis which has got abortive

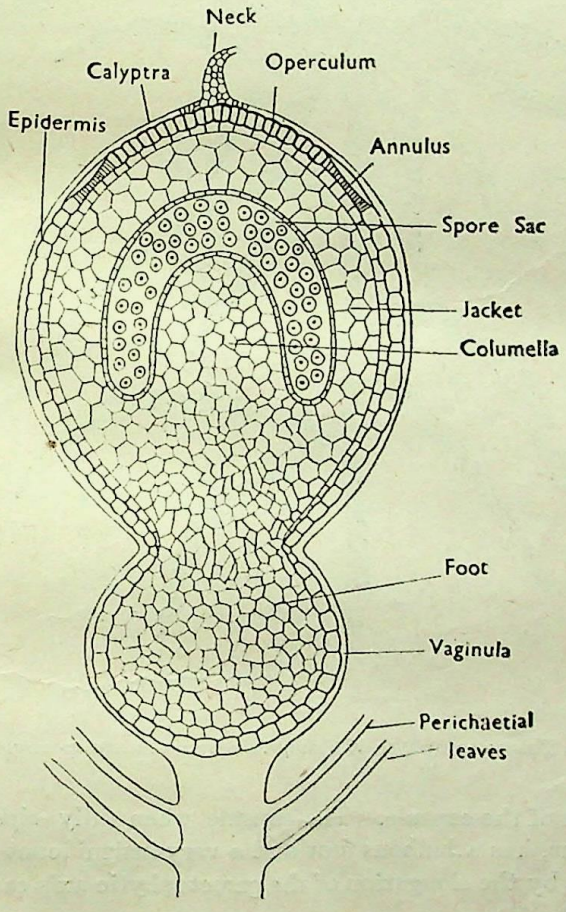

FIG. 37. L. S. of the capsule of *Sphagnum*.

stomata. The latter possess guard cells with no chloroplasts. Chloropyhyll is, however, present in rest of the cells. It indicates that sporophyte

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is not wholly dependent on the gametophyte for its nourishment. Some cells surrounding the capsule near the apex form **operculum**. Seta does not elongate much. It remains very short. The capsule remains surrounded by calyptra which is formed by the archegonial wall. The latter's lower portion gives rise to a sac like structure, the **vaginule** which

FIG. 38. The gametophyte of *Sphagnum* with mature sporogonia.

encloses the foot of the capsule. The capsule when fully ripe is brown or black in colour, has a bulbous foot and a very insignificant seta. It is pushed upwards by the elongation of the gametophytic axis called **pseudopodium** (Fig. 38).

When mature, it ruptures violently. The operculum is thrown out and the spores are disseminated several inches upwards. According to Nawaschin (1897) this violent discharge of spores is brought about by air pressure developed inside the spore sac.

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Structure and germination of the spore. As usual, each spore mother cell in the capsule divides twice, first being a reduction division, and produces four haploid spores which in the beginning are arranged in a tetrahedral fashion (Fig. 39, A). Each spore is uninucleate and possesses two walls—an outer exine and an inner intine (Fig. 39, B). It germinates within 2—5 days provided the conditions are congenial. During germination it sends out a small cellular filament (Fig. 39, C, D) which then gives rise to a thallose **protonema** only one cell thick. The protonema later on becomes lobed and develops rhizoids in the posterior portion (Fig. 39,E). The marginal cells of the protonema may give rise to a filament and the latter may form secondary protonema. According to Rhuland (1924) protonema may multiply in this manner. Finally each protonema gives rise to a new plant.

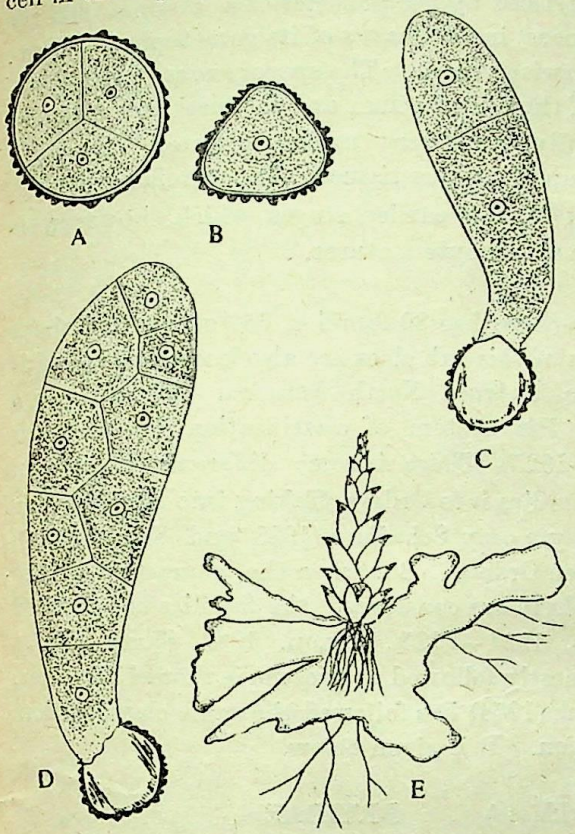
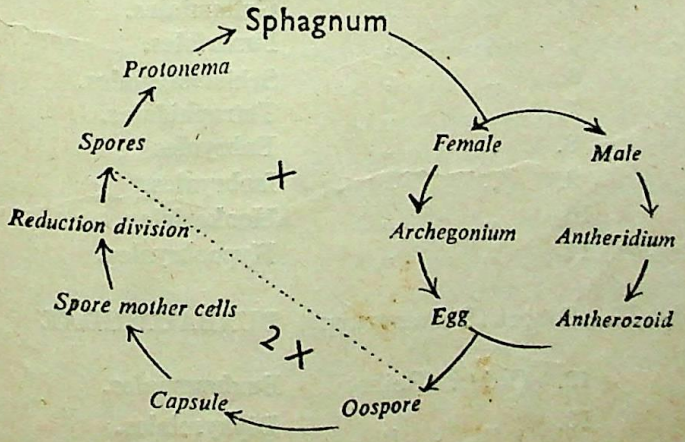


FIG. 39. A-D, germination of the spore of *Sphagnum*. E, thalloid protonema with rhizoids and leaves.



Life cycle of *Sphagnum*.

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Sub-class. EUBRYA.

The sub-class is characterized by the presence of a distinct mid-rib (more than one cell in thickness) in the leaves of its gametophyte. However, the leaves are not otherwise veined. The sporogenous tissue develops from the outer region of the endothecium and it does not make an arch over columella. Generally seta is very much elongated. Capsule is highly evolved and is made up of various tissues. The cap like structure, operculum, is vey prominent in the earlier stages which, however, is replaced by peristome as the sporophyte matures.

Classification. The sub-class has 80 families, 650 genera and about 14,000 species. Fossil species of this sub class are also known and according to Steere (1946) they are all from North America. Fleischer was the first to classify *Eubrya*. His system of classification was followed *in toto* by Brotherus (1924—1925). There is some difference of opinion regarding the grouping of families into Orders. Taking into consideration the characters of the sporophyte only Schaffner (1938) and Sharp (1939) divided the families into seven Orders. But when the characters of the gametophyte and the sporophyte are considered, the families are grouped into 14 Orders (Brotherus, 1924—1925., Dixon. 1932, Sharp, 1939.). However, the classification mostly followed at present is that of Fleischer, Dixon and Wettstein. Reimer (1954) has followed the same classification, though with slight modification. It is given below.

Sub-class (Unterklasse) **BRYIDAE.**

I. Cohort (Reihengruppe) **EUBRYIIDAE**

1. Order. (Reihe) **Fissidentales.**
2. ,, ,, **Dicranales.**
3. ,, ,, **Pottiales.**
4. ,, ,, **Grimmiales.**
5. ,, ,, **Funariales.**
6. ,, ,, **Schistostegiales.**
7. ,, ,, **Tetraphidales.**
8. ,, ,, **Eubryales**
9. ,, ,, **Isobryales.**
10. ,, ,, **Hookeriales.**
11. ,, ,, **Hypnobryales.**

II. Cohort (Reihengruppe) **BUXBAUMIIDAE**

12. Order. (Reihe) **Buxbaumiales.**
13. ,, ,, **Diphysciales.**

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III. Cohort (Reihengruppe) **Polytrichiidae.**

14. Order. (Reihe) **Polytrichales.**
15. ,, ,, **Dawsoniales.**

The Order *Funariales* comprises five families, 206 genera and about 356 species.

The families are.

1. *Gigaspermaceae*
2. *Funariaceae.*
3. *Disceliaceae.*
4. *Oedipodiaceae.*
5. *Splachmaceae.*

Only *Funaria* belonging to the family *Funariaceae* will be discussed.

Systematic position

Bryophyta.
Musci.
Eubrya.
Funariales.
Funariaceae.
Funaria.

Occurrence. The first reference to *Funaria* was made in the appendix to Ray's Synopsis in 1690. To Linnaeus it was known as *Mnium hygrometrica.* It was discovered in 1791 by Schreber and appeared in the 8th Edition of Linnaeus's "*Genera Plantarum*". The word *Funaria* is derived from a Latin term '*Funis*', means a rope and it refers to the characteristic twisting of seta in the moss when it is dry. The name *Funaria hygrometrica* was first coined by Sibthorp in his "Flora Oxomensis" (1794). Hedwig (1801) used the same term in his "Species Muscorum".

It has the distinction of being cosmopolitan in distribution and includes about 117 species. It is found on soil, on walls, and on the lands which have been burnt by fire. It grows vigorously in compact masses and within a very short period it occupies a vast area. However, the colonization depends upon the various habitats and accordingly it may be rapid or slow. For example growth of the moss may be rapid on moist bare soil and on a ploughed field, while it is slow on the rocky surface. This fact has been demonstrated experimentally true by Sharp (1939). *F. fascicularis* is found in fallow fields, *F. muehlenbergii* occurs on rock ledges and *F. attenuata* and *F. obtusa* are common in peaty banks. *F. hygrometrica* is a common moss on Indian Hills. Bruhl reported 15 species from this country.

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Structure. The short erect bright green coloured plants of *Funaria* are differentiated into rhizoids, stem and leaves (Fig. 40).

FIG. 40. Habit of *Funaria*.

Rhizoids. They are hyaline or whitish, branched multicellular thread like structures arising from the base of the plants. The septa are oblique. The colour of the rhizoids in the later stages becomes brown or red. Their function is the same as those of the roots in *Phanerogams i. e.* fixation of the plant and absorption of the food.

Leaves. The bright green membranous ovate leaves are spirally arranged on the stem. Each leaf is more or less sessile and possesses a well defined and distinct mid-rib.

In a transverse section the leaf shows two wings on either side and a central strand. The so called wings on either side contain chloroplasts and therefore conveniently carry on carbon assimilation. The cells in the middle carry on conduction (Fig 41). A very interesting phenomenon

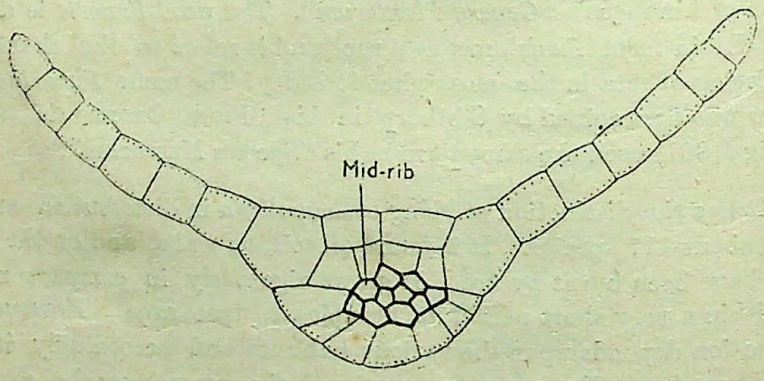

FIG. 41. T. S. of the leaf of *Funaria*.

of division of the chloroplast can easily be seen in the leaves of this moss. Here the chloroplast undergoes divisions even when the leaves reach complete maturity.

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Stem. It is green, delicate and branched (not very often). In a transverse section it exhibits the following structures (Fig. 42).

1. **Epidermis.** It is the outermost layer. Its cells are thin (may be thick occasionally). It is single layered (may be double layered at certain places) and contains chloroplast. It lacks cuticle and stomata.

2. **Cortex.** It is multilayered. It is made up of parenchymatous cells which may be thin or thick. The "leaf trace" may be present which runs diagonally from the leaf to the central cylinder.

3. **Central cylinder.** The middle region is occupied by slightly smaller cells (smaller than the cells of the cortex). which are slightly thick walled. Bower (1933) showed that whatever may be the habitat of the moss small amount of water moves up through this region. Magdefrau (1935) and Ignold (1955) regard it as a conducting region.

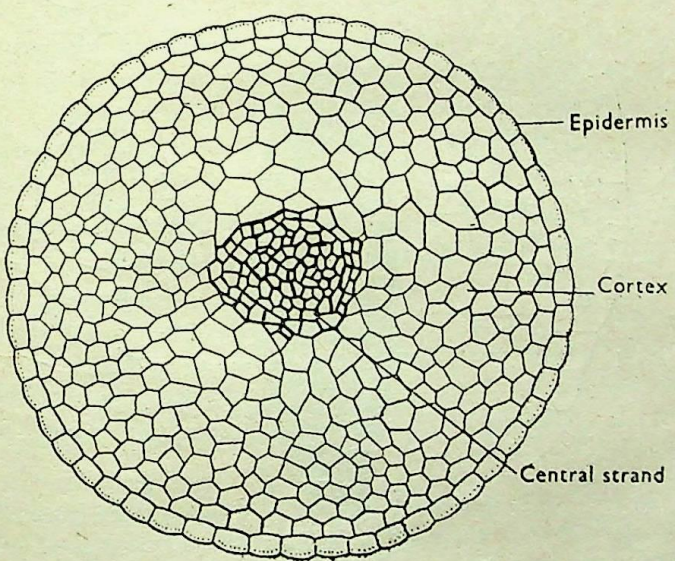

FIG. 42. T. S. of the stem of *Funaria*.

Reproduction. It is brought about by two methods.

1. *Vegetative.*
2. *Sexual*

1. **Vegetative multiplication.** In mosses vegetative multiplication is a very common phenomenon. According to Smith some mosses multi-

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ply abundantly only by vegetative means. This may take place by any of the following methods.

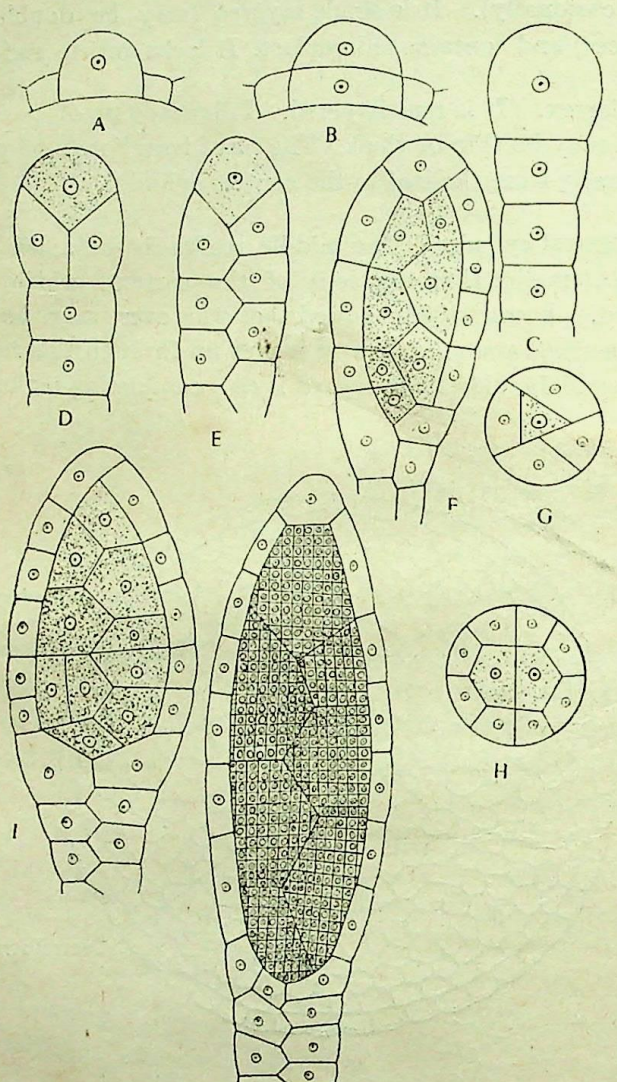

FIG. 43. Stages in the development of the antheridium of *Funaria*. A—E, formation of antheridial initial. F, very young antheridium with jacket cells and androcyte mother cells. G, H. T- S. of the antheridium. I, J, antheridia with a short stalk and sterile jacket. Inside are androcytes.

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A. **Death and decay of the rhizoids.** The rhizoids run prostrate and erect branches are given out from them. Sometimes the rhizoids die out and erect branches constitute a single independent plant.

B. **Gemmae.** Small multicellular bodies may be formed at the tips of the leaves, at the apex of the stem or on the rhizoids. When gemmae are subterranean they are called **bulbils.** Each gemma, when detached, gives rise to a new plant. Berkley (1941) reported the formation of such gemmae at the apex of the protonemal branches.

C. **Primary protonema.** It is formed by the germination of a spore. It consists of many buds which later on give rise to moss plants. Increase in the number of protonema increases the number of plants also. If the cells in a protonema die out they give rise to small fragments and each fragment on germination forms a new individual.

D. **Secondary protonema.** When protonema arise from any part of the plant (but not from the spores) they are called secondary protonema. Such protonema do occur in *Funaria* particularly on wounded portions. On germination they give rise to new plants.

2. **Sexual.** The sexual reproduction is brought about with the help of male and female organs of reproduction called antheridia and archegonia respectively. Campbell's observation that the plants of *Funaria* are dioecious is erroneous and it is now an established fact that the plants are strictly monoecious, though autoceous (Boodle and Brown). At maturity the male branches appear brownish in colour if seen against light. The female branches are evergreen.

Development and structure of antheridium. A superficial cell at the apex of the male branch acts as an **antheridium initial** (Fig. 43, A). It slightly buldges out and then divides into two—an outer cell and an inner cell (Fig. 43, B). The former further divides and forms a row of two or three cells (Fig. 43, C). The terminal cell in this row acts as an apical cell with two cutting faces (Fig. 43, D). It now cuts off 5—15 segments. The inner cell finally gives rise to the lower portion of the stalk of the antheridium (Fig. 43, E).

Before the cessation of the activity of the apical cell, divisions start in the fourth or the fifth segment and the first division is diagonally vertical. One of the smaller cells is the jacket initial. The bigger one

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again divides and gives rise to another **jacket initial** and a **primary androgonial cell**. The latter appears triangular in a cross section (Fig. 43, G). The upper segments (cut off by apical cell) later on divide in the same way. Thus the disivions which start from the lower side eventually proceed to the upper region. Finally single androgonial cell may be seen surrounded by two jacket initials.

The primary androgonial cell divides and redivides and gives rise to many androcyte mother cells (Fig. 43, F–J). Now each androcyte mother cell forms two androcytes and according to Allen (1912) the division is not diagonal (Unlike the *Hepaticae*). According to the same author (1912, 1917), the formation of antherozoids from the androcyte is exactly similar as in *Hepaticae*. The jacket cells also divide but only radially and thus a single layered wall surrounds the antheridium (Fig. 43, J, H).

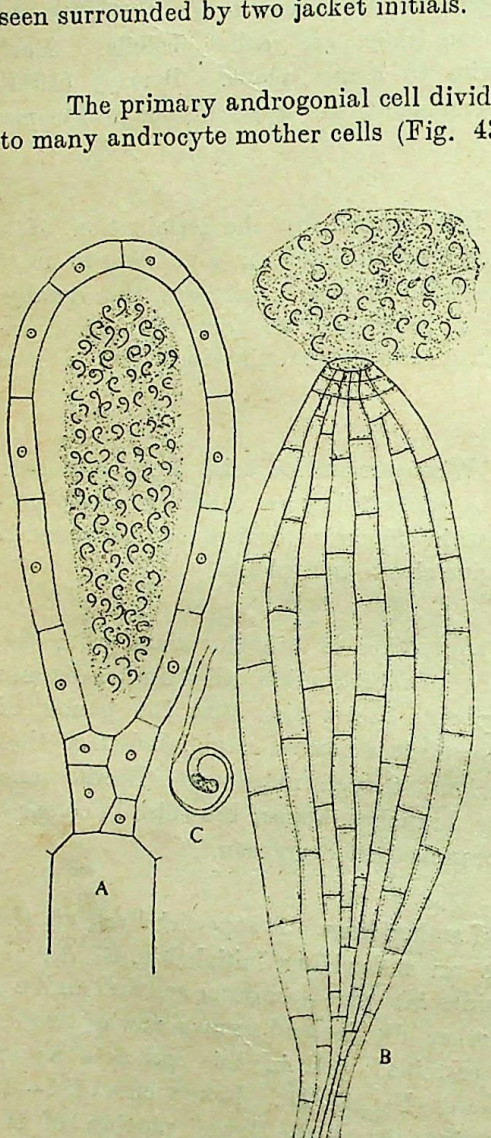

FIG. 44. A, L. S. of the antheridium of *Funaria* showing many antherozoids. B, liberation of antherozoids. C, single biciliate antherozoid.

Liberation of the antherozoids. The club shaped antheridium has a short stalk and an operculum. It contains numerous antherozoids (Fig. 44, A). Water is indispensable for the liberation of the antherozoids. The antheridium absorbs water and a hydrostatic pressure is created inside. At the same time the jacket cells also become turgid. This pressure is sufficient to force the operculum to open. As soon as it opens, the whole mass of the antherozoids comes outside (Fig. 44, B). Each antherozoid is uninucleate and biciliate (Fig. 44, C).

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The antheridia are closely associated and surrounded by many sterile structures, the **paraphyses.** Each paraphysis is an elongated structure with four or five long narrow cells joined end to end. (Fig. 45) The terminal cell of the paraphysis is globose. Goebel (1905) referred to the functions of these structures. According to him these structures help in water conservation and are also meant for the protection of the antheridia against external environments. Resse (1955) referred to these structures as a means of vegetative propagation. Rarely, the lowermost cell gives rise to protonema.

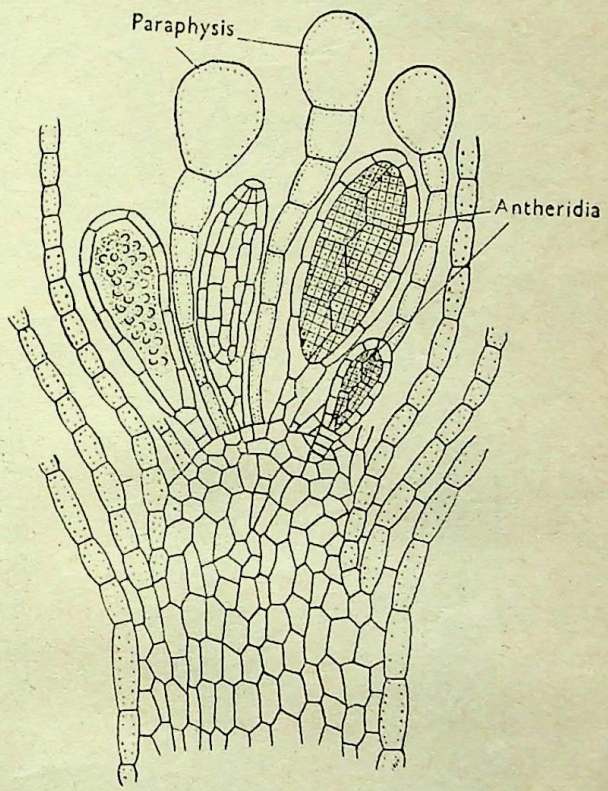

FIG. 45. L. S. of the male branch of the moss showing antheridia and paraphyses.

Development of the archegonium. The archegonium develops from an apical cell, which in the earlier stages, has two cutting faces (Fig. 46, A–C). It cuts off four to eight segments. These segments further divide and finally give rise to the stalk of the archegonium. According to Holfesty (1904), Bryan (1917) and Burr (1939) the apical cell abruptly changes and develops three cutting faces (Fig. 46, D,E). Each face cuts off a single segment and thus three peripheral cells, now called **peripheral initials,** encircle the former apical cell, now known as **axial cell.** The peripheral cells divide vertically and so six **jacket initials** are produced. In the meantime the axial cell divides transversely and gives rise to a primary cover cell and a central cell (Fig. 46, F, G). The latter again divides transversely and forms a **primary canal cell** and **a venter cell** (Fig. 46, H). The former (also jacket initial) gives rise to the median and the lower portion of the neck

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while the upper portion is formed by the primary cover cell. The venter cell divides and gives rise to a ventral canal cell and an egg (Fig. 46, I-L).

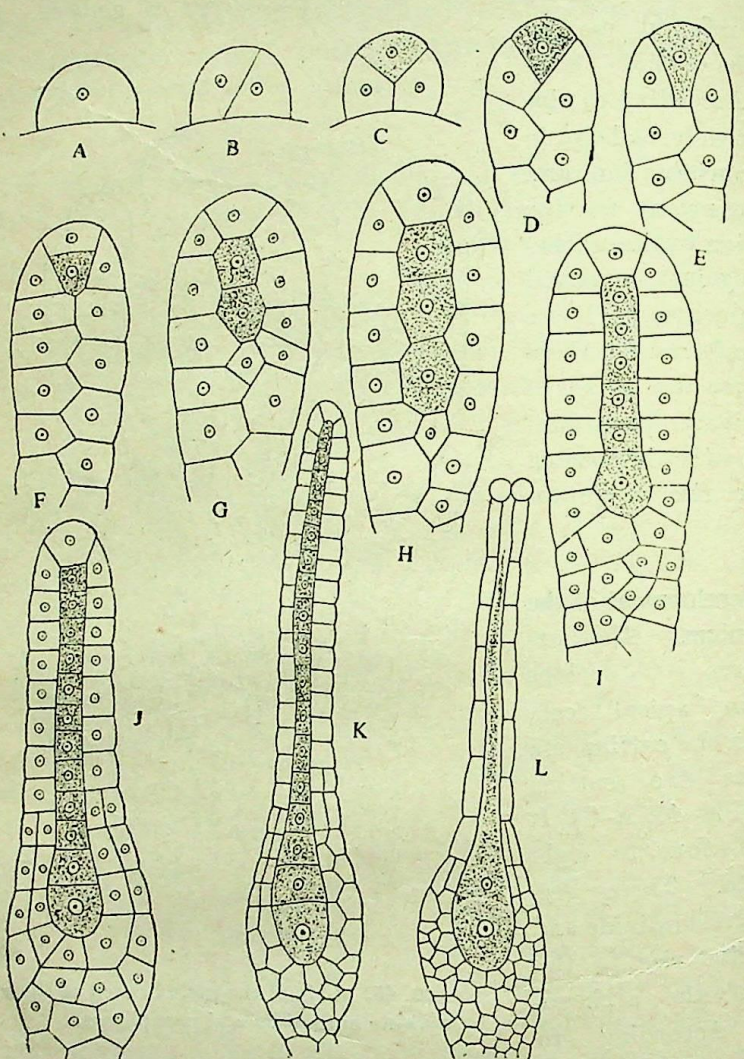

FIG. 46. Stages in the development of the archegonia of *Funaria*. A-E, formation of archegonial initial. F, first division of the archegonial initial. G, formation of ventral canal cell and egg. H—K, development of fully mature archegonium. L, archegonium ready for fertilization.

Archegonium thus becomes an elongated flask shaped structure with a long neck and a swollen venter. The neck is single layered and consists of six or more neck canal cells while the venter possesses a ventral canal

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cell and an egg and is double layered. At the top there are cover cells (Fig. 46, K).

Fertilization. At the time of fertilization the neck canal cells disintegrate and form a mucilaginous mass. As the water is absorbed, the mucilage swells and the neck opens. Thus a clear passage is formed for the entry of the antherozoids. Many such archegonia may be seen if a L. S. of the female branch is cut. Along with these female organs are sterile hairs (Fig. 47). No doubt water is indispensable for fertilization, the movement of the antherozoids is chemotactic. Many antherozoids are attracted but ultimately it is only the one which fertilizes the archegonium. The nucleus of the male unites with the nucleus of the female and it results in the formation of an **oospore.**

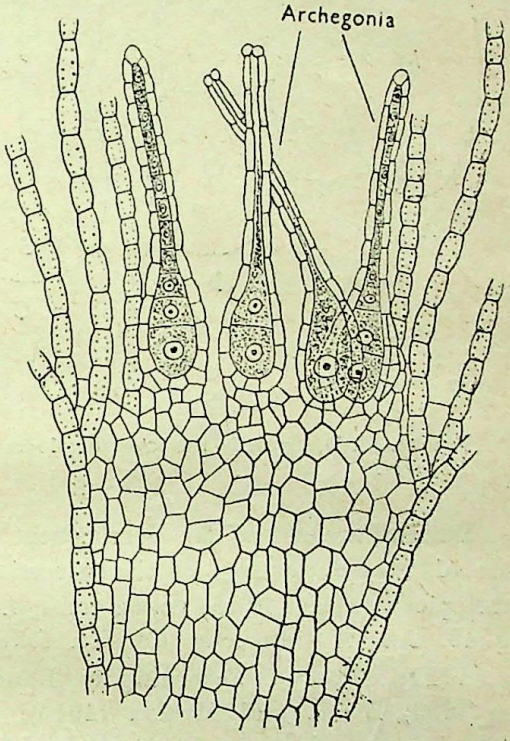

FIG. 47. L. S. of the female branch of the moss showing archegonia and sterile hairs.

Post fertilization stages. Immediately after fertilization the oospore increases in size (Fig. 48, A) and divides into two by a transverse wall forming an **epibasal** (upper one) and a **hypobasal** (lower one) cell (Fig. 48, B). Soon afterwards the epibasal cell divides by two diagonal divisions into an apical cell with two cutting faces. The same thing happens in the hypobasal cell. Thus young embryo of this moss possesses two growing points (Fig. 48, C). The apical cell in the epibasal region cuts of cells right and left and finally develops capsule and most of the portion of seta. Remaining portion of the seta and foot are developed from the hypobasal region (Fig. 48, D).

In the earlier stages the development of the embryo is accompanied by the development of the surrounding tissue which forms the **calyptra.**

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The latter structure, however, gets broken by the elongation of the sporophyte.

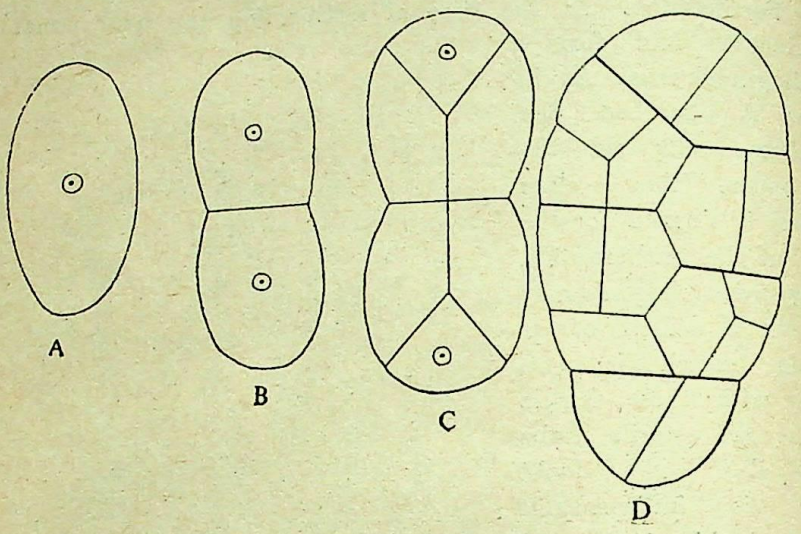

FIG. 48. A-D, stages in the early development of the sporogonium of *Funaria*.

Detailed account of the development of the capsule. The capsule, as already stated, develops by the successive divisions of the apical cell in the epibasal region of the young embryo. The first division is vertical (Fig. 49, A). A transverse division follows and thus a quadrant is formed (Fig. 49, B). According to Blomquist and Robertson (1941), Burr (1939), Evans and Hooker (1915), Wenderoth (1931) and Wijk (1929) each part of the quadrant now undergoes anticlinal division in such a way that one daughter cell in each quadrant is triangular and the other is more or less rectangular (Fig. 49, C). Now periclinal divisions follow in each quadrant and so finally four cells are differentiated in the middle surrounded by eight peripheral cells (Fig. 49, D). The former give rise to the **endothecium** while the latter constitute the **amphithecium**. In fact the endothecium and the amphithecium are the chief constituents which ultimately form the different tissues of the capsule. The further developments in different parts of the capsule are slightly complicated, though very systematic and regular. For the sake of convenience the developments in the different parts of the capsule may be discussed separately.

1. Developments in the central fertile region.
2. Developments in the apical region (Thecae).
3. Developments in the lower region (Apophyses).

1. **Developments in the central fertile region.** In all the four central endothecium cells diagonal or vertical (anticlinal) divisions take place

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followed by periclinal divisions resulting in the formation of four inner endothecial cells and eight peripheral endothecial cells (Fig. 49, E). The former divide twice and give rise to sixteen cells which finally constitute **columella.** The eight peripheral cells divide radially and periclinally and thus form two rings. The cells of the outer ring once again divide radially and form archesporium while the cells of the inner ring, adjacent to columella, constitute the inner spore sac (Fig. 49, F). The cells of the archesporium give rise to spore mother cells which finally convert into spores.

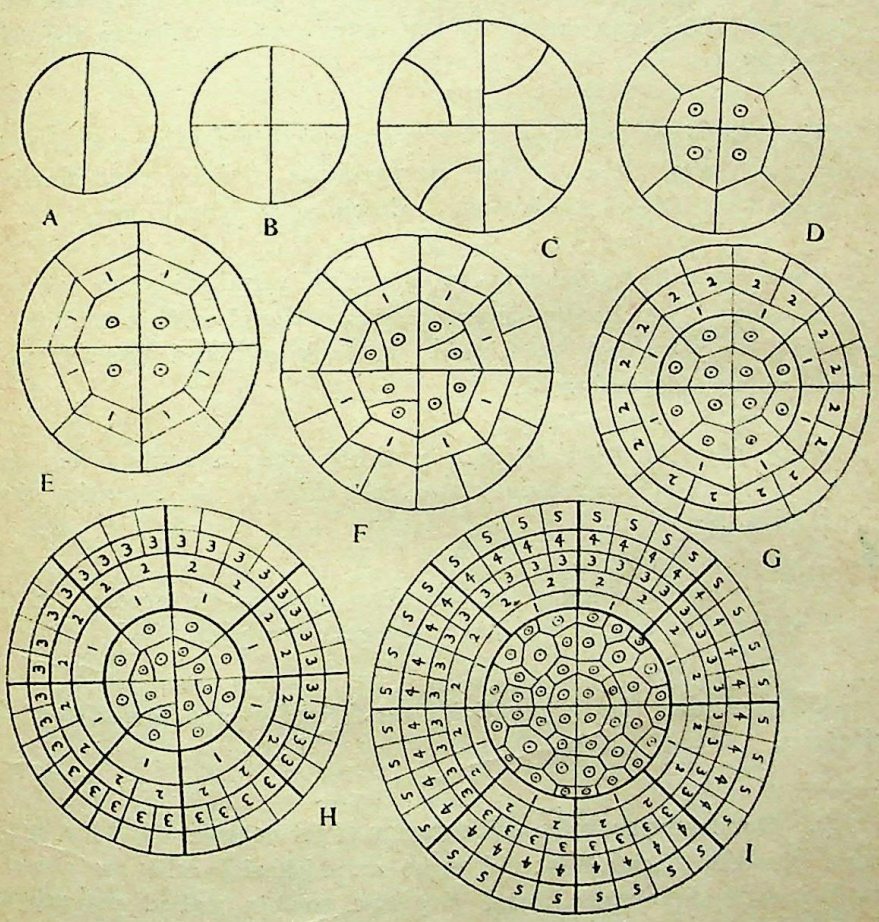

FIG. 49. Transverse sections of the capsule of *Funaria* taken from different levels. A-D, differentiation of amphithecium and endothecium. E-I, development of rings.

According to Blomquist and Robertson (1941), Burr (1939), Evans and Hooker (1913) and Wenderoth (1931) the divisions in the amphithe-

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cium are very systematic and have a definite pattern. Goebel called this pattern the "Grundquadrat" or Fundamental square method. The amphithecium divides periclinally and thus two concentric rings are formed. The inner ring may be referred to as the first ring (Fig. 49, E, F). Cells of the outer ring now divide anticlinally followed by periclinal divisions almost immediately. Thus two rings of sixteen cells are formed. The inner ring is called the second ring (Fig. 49, G). The cells of the outer ring again divide anticlinally and periclinally and so two concentric rings of thirty two cells are again formed. The inner one is known as the third ring (Fig. 49. H). The outer cells further divide in a periclinal fashion and so two rings of thirty two cells are again formed. The inner one is termed the fourth ring while the outer one constitutes the fifth ring (Fig. 49, I).

The cells of the first ring divide in an anticlinal fashion and give rise to thirty two cells. It is followed by periclinal divisions and finally a four layered outer spore sac is formed, which lacks chloroplast.

The cells of the second ring elongate radially and so air space appears in these cells. These become laterally separated and contain chloroplast. Later on there is a transverse division in each cell and thus a filament of three or four cells is formed.

The cells of the third ring remain thirty two in number but only one cell in thickness (occasionally two cells thick). At maturity these possess chloroplast.

The fourth ring becomes two or three layered on account of the periclinal divisions but its cells never possess chloroplast.

Cells of the fifth ring divide anticlinally and constitute the epidermis.

2. **Developments in the apical region of the capsule.** In the upper region four endothecial cells and eight amphithecial cells are present. The former divide repeatedly and give rise to thin walled parenchyma which is continuous with the columella of the fertile region. The amphithecium, as usual, forms five concentric rings of which the first ring (32-celled) gives rise to inner **peristomial layer** (after anticlinal divisions) and the second ring gives rise to the outer peristomial layer. Cells of the third and the fourth ring become three layered and form operculum while the cells of the fifth ring form the epidermis. The cells of the epidermis at the base of the operculum enlarge radially and constitute the **annulus.**

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3. **Developments in the lower region of the capsule.** The endothecial cells in the apophyses form the conducting region. Amphithecium develops into spongy chlorophyll and epidermis. The latter possesses stomata.

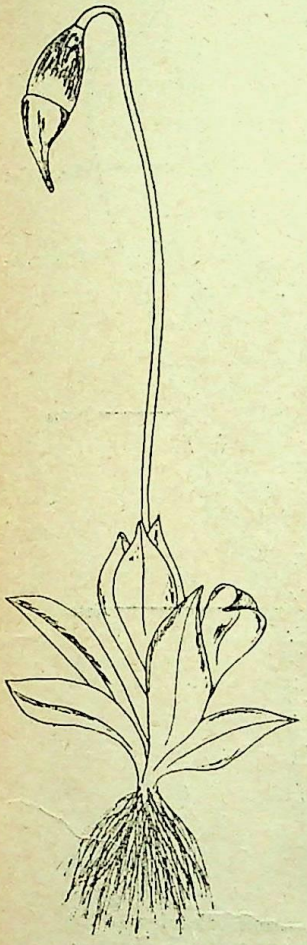

FIG. 50. Gametophyte of *Funaria* bearing the sporophyte. Long seta and capsule with operculum are visible.

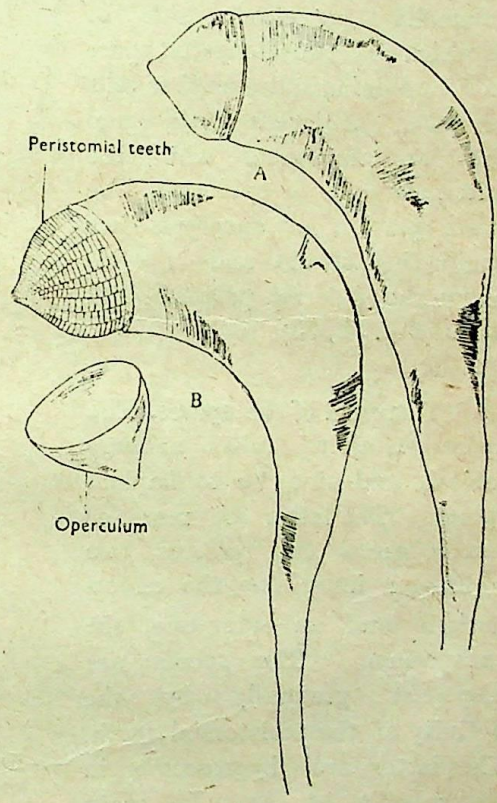

FIG. 51. *Funaria* capsule. A, with operculum and B, operculum removed to see the peristomial teeth.

Thus the sporophyte of *Funaria* is differentiated into foot, seta and capsule. The foot is small and not very well developed. Its function is to absorb water and other food materials (Fig. 50).

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The seta is an elongated thread like structure, the function of which is more or less mechanical. The pear shapel capsule with a hood of broken calyptra is carried above by seta. The essential parts of the capsule are, **operculum**, the cap like structure which in the later stages is replaced by **peristome** or peristomial teeth that bring about the dispersal of the spores (Fig. 51, A, B) and columella on either side of of which are two elongated spore sacs containing spore mother cells or spores. Adjacent to the spore sacs are air spaces while the outermost layer is epidermis. The lower portion or **apophysis** has conducting strand and in this region the epidermis possesses stomata (Fig. 52, 53).

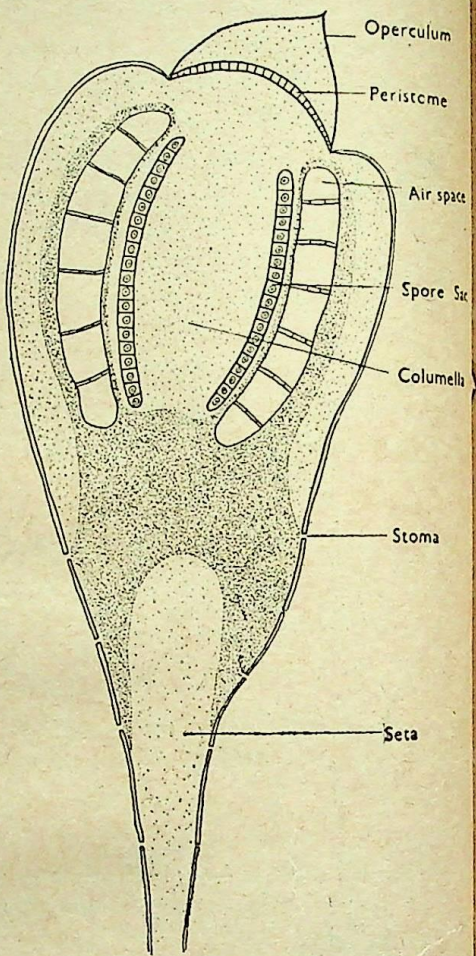

FIG. 52. Diagrammatic view of the capsule of *Funaria* in a L. S.

Dispersal of the spores. The spore mother cells undergo meiosis and give rise to haploid spores. The latter are more or less spherical and possess two walls—an inner one, the endosporium and an outer one, the exosporium. The spores are dispersed gradually by the activity of the peristomial teeth. The latter are hygroscopic in nature (Fig 54, A). In moist condition they remain inside and their tips remain in touch with the spores (Fig. 54, B). When the conditions are dry they come outside, their tips laden with spores (Fig. 55, C). Movement of wind or even the mild breeze is quite sufficient to dislodge these spores (Fig. 54, D) and thus they are taken to far off places. The peristomial teeth remain active till the spores are dispersed (Fig. 55, A, B).

Germination of the spores. The first account of the germination of the spores was given by Hedwig in 1782. Further investigations on

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this juvenile phase of the moss were carried out by Muller (1874),

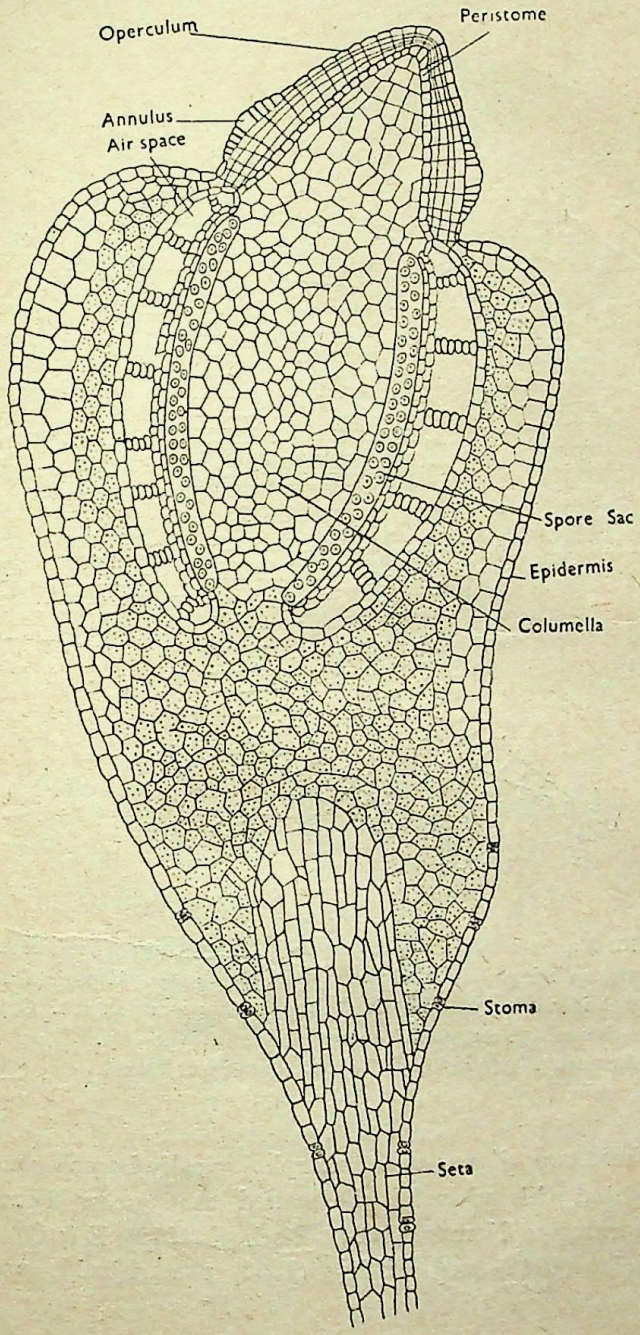

FIG. 53. L. S. of the capsule of *Funaria* showing detailed anatomy.

Sachs (1875) and Goebel (1882). According to the these workers

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the spore germinates into a primary protonema which has green filaments containing chlorophyll and pale or brown rhizoids. They

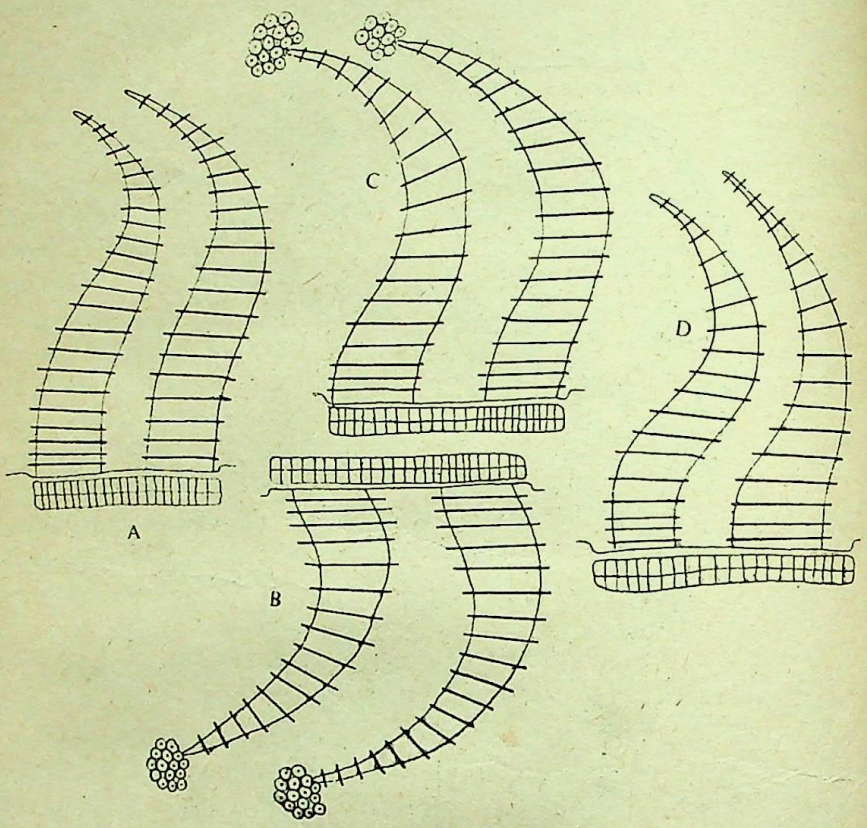

FIG. 64. Peristomial teeth and their hygroscopic movements in order to bring about the dispersal of the spores. A, peristomial teeth in normal condition. B, the teeth moving inside. C, the teeth coming out with spores laden at the tip. D, spores taken away by wind and the teeth again left barren.

regarded these two filaments as morphologically homologous. Correns (1899) accepted this view but he called the green filaments chloronema. According to Nemec (1904), Bischoff (1912), E & O. Pringsheim (1935), Heitz (1942) and Fitting (1950) the rhizoids are positively geotropic.

According to Sironval (1947) there are two protonemal stages. First is just after germination when green filaments are produced which he called **chloronema** and the second he termed **caulonema**. The latter, according to him, has rhizoidal characters.

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Bopp (1952, 1954, 1955) supported Sironval. Van Andel (1952) could not see caulonema of Sironval. According to Allsopp and Mitra there is "no indication of the distinct stages 'chloronema' and

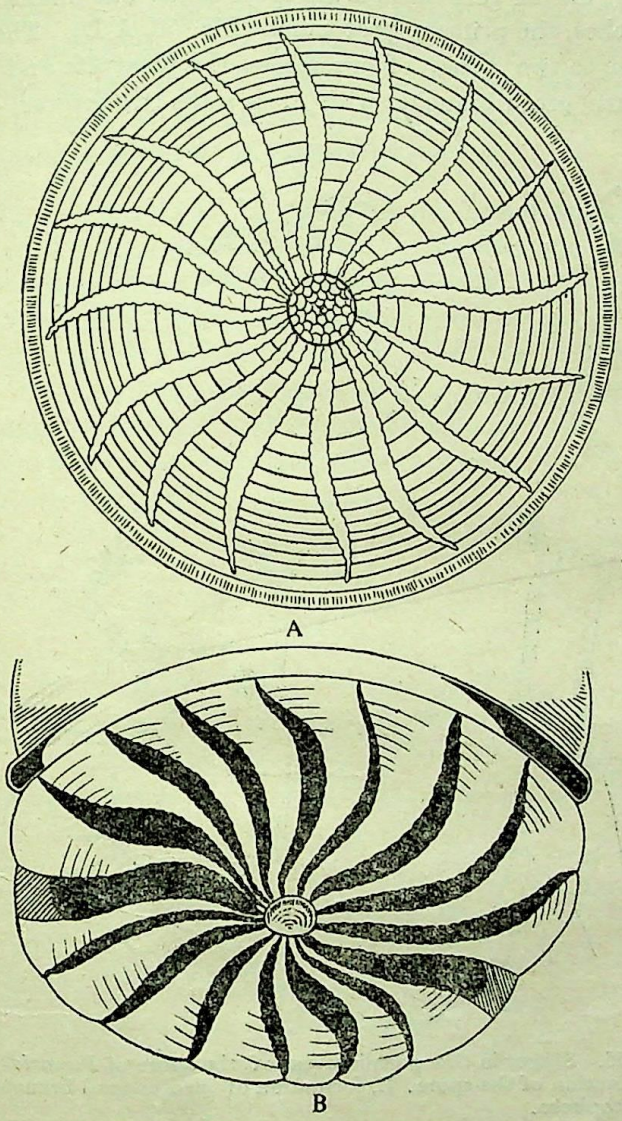

FIG. 55. Peristome of *Funaria*. A, peristome seen from above. B, another view of the peristome.

'caulonema' identified by Sironval (1947)". According to the same workers "the characteristic of caulonema as described by Sironval are clearly those of the normal well grown protonema. They are certainly not associated with a distinct morphological phase, but are

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probably indicative of a certain nutritional status of the protonema". The bud formation, according to these workers, is not restricted to the caulonema alone.

Anyhow, during germination the spore sends out filamentous multicellular branches, the primary protonema (Fig. 56, A-D). The protonema then gives rise to two types of branches—the prostrate and the upright (**heterotrichous**) green branches with cross walls (transverse), the chloro-

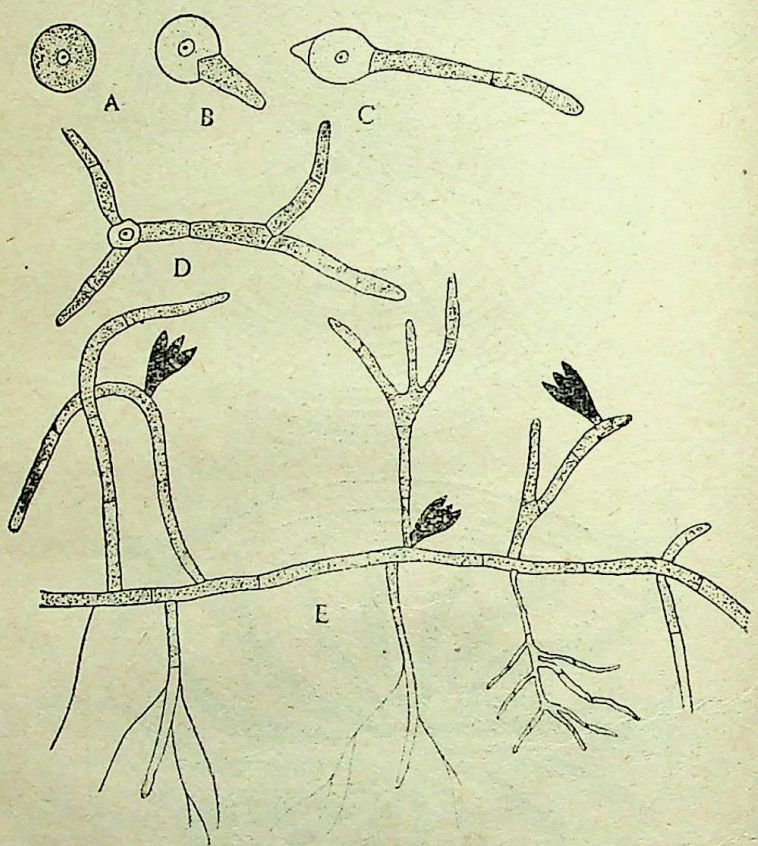

FIG. 56. Stages in the germination of the spore of *Funaria*. A—D, germination of the spore. E, formation of protonemal branches and gametophore.

nema and the branches which go into the soil, possess little chloroplast or leucoplast and have oblique cross walls. The protonema develops buds which finally give rise to new moss plants (Fig. 56, E). After many buds have developed and leafy gametophytes are produced, the primary protonema degenerates.

Alteration of generations. The moss plant belongs to the gametophyte generation. It bears sex organs, the antheridia and the archegonia

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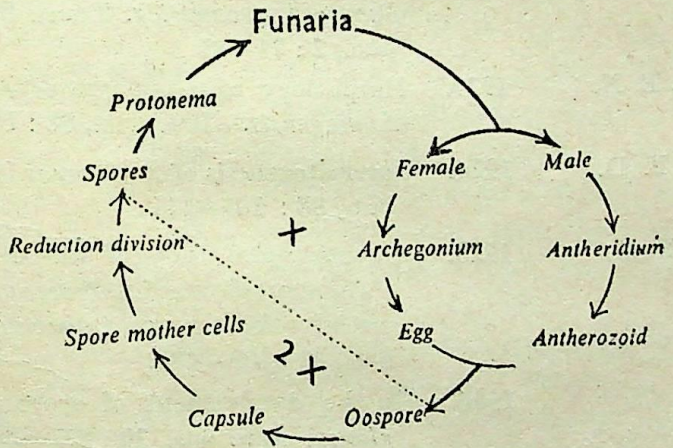
Both the sex organs are haploid in nature. The antheridia give rise to the **antherozoids** while the archegonia possess **egg**. At the time of fertilization the male and the female nuclei unite resulting in the formation of an oospore. The formation of the latter structure is the end of the gametophyte generation. An altogether new generation starts with the formation of the diploid **oospore** and it is called the sporophyta generation. During post fertilization stages, the sporogonium or the capsule possesses spore mother cells. The latter after two successive divisions (one of the divisions is reductional) give rise to spores, which are haploid in nature (consult life cycle of *Funaria* at the end).

Thus the life history of moss exhibits two clear and very distinct phases. Haploid phase which is before fertilization and after reduction division and diploid phase which is after fertization and before reduction division. The former (Haploid phase) constitutes the gametophyte generation and the latter (diploid phase) corresponds to the sporophyte generation. The gametophyte generation gives rise to the sporophyte generation and the latter in its turn gives rise to the gametophyte generation again. That is the two generations alternate with each other and this is called the alternation of generations.



Life cycle of *Funaria*.

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PTERIDOPHYTA

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CHAPTER 5

PTERIDOPHYTA

Introduction. This division includes higher Cryptogams that are also called "**Vascular cryptogams**" The term "*Cryptogam*" is an old name suggested by Linnaeus (1754) for all non-flowering plants in which sexual reproduction was unknown at one time. The term "*vascular*" refers to the presence of conducting tissues *i. e.*, xylem and phloem for the conduction of water and food. Their fossil record shows that they were abundant forming the dominant vegetation of the earths flora in the Paleozoic and Devonian age about 350,000,000 years back. The present day plants are small but they have descended from tree-like forms which produced extensive forests in the "**Coal Measures**". The flowering plants have succeeded them and have relegated them to a lower position in the plant kingdom. Thus they are regarded the most primitive of the fossil and living vascular plants.

They show certain affinities with Bryophytes and some of them with Spermatophytes thus occupying an intermediate position between the two.

Characters showing similarity with Bryophytes.

(a) Terrestrial mode of life.
(b) Presence of moisture for accomplishing fertilization.
(c) Alternation of generations.
(d) Presence of a sterile jacket around the sexual organs.
(e) Parasitic nature of the young sporophyte (partially or wholly) on the gametophyte.

Characters showing Similarity with Spermatophytes.

(a) Diploid sporophytic plant body differentiated into root, stem and leaves.
(b) Mature sporophyte independent of the gametophyte.
(c) Lodging of spores in the sporangia on the leaves. The spores may be homosporous or heterosporous.

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(d) Vascular tissues are very well developed for conducting water and food.

Habit and Habitat. Their form is variable, though there are two general types.

(a) **Megaphyllous types.** Including plants with small stems and large leaves e. g., Ferns.

(b) **Microphyllous types.** Comprising plants with large stems and small leaves *e. g.*, "Horsetails" (*Equisetum*) and "Club mosses" (*Selaginella*).

The plants are either small sized annuals, or perennials reaching a large size and usually thrive well in cool, damp, shady places, though some develop well in sandy soils especially in xeric climates, behaving as xerophytes. The branching of stem shows a range of variation. It may be monopodial, dichotomous or with a tendency to dichotomy; axillary branching such as that of spermatophytes does not occur.

Anatomical Structure.

Stem. It displays an outer cortex consisting of parenchyma, sclerenchymatous hypodermis, and a central stele ranging from a protostelic to a polycyclic condition containing xylem and phloem. The latter usually surrounds the xylem. The xylem is made up of tracheids and the phloem of sieve tubes.

Leaves. These are either simple or pinnately compound. In megaphyllous types, they consist of a leaf-blade or lamina and a petiole. The microphyllous types are simpler than the megaphyllous and are sessile. The latter show the differentiation of the mesophyll into palisade and spongy tissues.

Roots. The adventitious roots usually arise in acropetal succession on the stem or in many ferns on petioles, their branching is monopodial or dichotomous. They show a **diarch** structure—which is almost constant throughout the Pteridophytes and hence regarded as a "**conservative organ**".

Reproduction. It takes place by **spores** which develop in **sporangia**. The sporangia are borne either on the leaves or in axils between the leaves and the stem. They are of two types, **leptosporangiate** which develop from a single superficial cell e. g., ferns and Marsiliaceae, or **eusporangiate**, which are developed from a group of cells, as is the case of most of the Pteridophytes. In both the cases, the sporangium develops **archesporium** from which **spore-mother-cells** are produced. These divide

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meiotically to form four spores. A sporangium when half developed consists of three parts : (1) The outer **wall** formed of one or more cell layers. (2) An inner **sporogenous mass** forming spores and (3) A middle **tapetum** formed of one or more layers of tabular cells, forming an investment round the sporogenous tissue. If the spores are of the same size, the plant is called **homosporous**, and if they are of different size, **heterosporous**. The small spores (**microspores**) are regarded male spores where as the larger spores (**megaspores or macrospores**) as female, and hence the sporangia are named accordingly. The spores on germination never reach a stage of differentiation into stem and leaf as seen in Mosses, but develop gametophytic **prothalli**, bearing sexual organs—the **antheridia** and **archegonia** in large numbers for reproduction. This is regarded as the **gametophytic** (sexual) generation, often referred to as "**oophyte**" by Goebel. The prothallium is a thalloid structure.

In Selaginellaceae and Isoetaceae the female prothallium is entirely developed inside the megaspore which it fills with its tissue, and only the archegonia come forth to the light through fissures in the outer coat of the megaspore. The microspores produce very rudimentary male prothallium producing only antheridia. These develop spermatocytes which in turn produce spirally coiled **sperms**.

The archegonia like those of Mosses, consist of **venter**, containing **oosphere** (egg) and **venter-canal-cell,** and a **neck** which is usually short and formed of 4 longitudinal rows of cells. The venter is enclosed in the tissue of the gametophyte, the neck only projecting above it. The neck contains two **neck-canal-cells**. When mature the two neck canal cells and venter canal cells are converted into mucilage, which swells considerably thus forcing open the four apical cells of the neck and is ejected. This results in the formation of an open passage leading from the outside to the oosphere. The ejected mucilage helps in attracting the motile sperms to the orifice of the neck. **Fertilization**, in all cases, is brought about by the agency of water, which causes the antheridium and archegonium to open and serves as a vehicle for the sperms. As a result, the sperms make their way tothe egg and coalesce with its protoplasm to form a diploid **oospore**. This marks the beginning of asexual **(sporophytic)** generation.

The first divisions of the embryo indicate the rudiments of the first root, the first leaf, and the apex of the stem, while a lateral outgrowth of the tissue of the embryo, the so called foot, is formed at the same time at the bottom of the venter of the archegonium. This draws the first nutriment for the embryo from the female prothallium. The venter of the archegonium grows vigorously at first in all except Selaginellaceae, and still encloses the embryo, but the latter at length emerges from it, leaving the foot for a time still in it to serve as an organ of suction. In

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this lies an indubitable analogy with the formation of the **calyptra** in the mosses. But while the sporophyte in Mosses is never more than a mere appendage of the gametophyte and looks to a certain extent like its fruit, the corresponding generation in the Pteridophytes develops into a tall, highly organized, independent plant which becomes detached from the prothallium and supports itself at an early stage. It is this sporophyte which is usually termed absolutely a *Fern*, or an *Equisetum*, or *Selaginella*, and which forms no sexual organs but numerous sporangia. Thus the life cycle shows a clear alternation of these two morphologically and physiologically different generations. It is clear, therefore, that the sporophyte has become the dominant phase of the life cycle.

Classification of the Pteridophyta. The classification of Pteridophytes is elaborate and somewhat complicated as it includes many fossil forms which are extinct and are no longer represented in the present flora. These revealed many facts concerning the status of some groups that are not expressed by living plants and hence their influence on classification is of paramount importance. There is no perfect and final classification of plants. Those systems which seem quite satisfactory today and are in use may be obsolete tomorrow and may be replaced by new ones. With the advancement of knowledge, they will be subject to changes as long as facts about them remain unknown.

There are various systems of classification, some disagree on basic principles whereas many of them differ in detail. Prantl, as early as 1874 divided the Pteridophyta into three classes : Filicinae, Equisetinae and Lycopodinae. The first and the third are further subdivided into Isosporae and Heterosporae. This system was adopted by Luerssen (1879), Eichler (1883). Van Tieghen (1883-84). The latter in his system included fossil plants too and also subdivided the Equisetinae into homosporous and heterosporous. With the publication of Engler and Prantl's **Die naturlichen Pflanzenfamilien** (1898-1900) the group was divided into four classes as follows :—

Class I. **Filicales**
- Filicales leptosporangiatae
  - Eufilicineae
  - Hydropteridineae
- Marattiales
- Ophioglossales

Class II. **Sphenophyllales**

Class III. **Equisetales**
- Euquisetales
- Calamariales

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Class IV. **Lycopodiales**
- Lycopodiales eligulatae
  - Lycopodineae
  - Psilotineae
- Lycopodiales ligulatae
  - Selaginellineae
  - Lepidophytineae
  - Isoetineae

Jeffrey (1910) on the basis of some anatomical characters, proposed that Pteridophytes should be abondoned and that the vascular plants should be sub-divided into two great primitive stocks : Lycopsida (consisting of Lycopodiales and Equisetales) Pteropsida (consisting of ferns, Gymnosperms and Angiosperms). This was adopted and modified by Zimmermann (1930). Eames (1936), Tippo (1942), Arnold (1947), Boivin (1956) and Berry (1920) classified vascular plants into seven "**phyla**" : Pteridophyta, Arthrophyta, Lepidophyta, Pteridospermophyta Cycadophyta, Coniferophyta and Angiospermophyta.

According to Bold (1957) the four series which composed the old division, Pteridophyta have been raised to divisional rank as follows :—

Division I. **Psilophyta**

Division II. **Microphyllophyta**
(Lycopsida or Lepidophyta of other authors)
- Aglossopsida—Lycopodium
- Glossopsida
  - Selaginellales
  - Isoetales

Division III. **Arthophyta**—Arthropsida—Equisetales
(Sphenopsida or Calmophyta of other authors)

Division IV. **Pterophyta**
(Filicinae of other authors includes all macrophyllous plants)
- Eusporangiopsida
  - Ophioglossales
  - Marattiales
- Leptosporangiopisda—Filicales

We have, for the sake of convenience, followed Arnold (1947) in the present text. He has classified the vascular plants, which have

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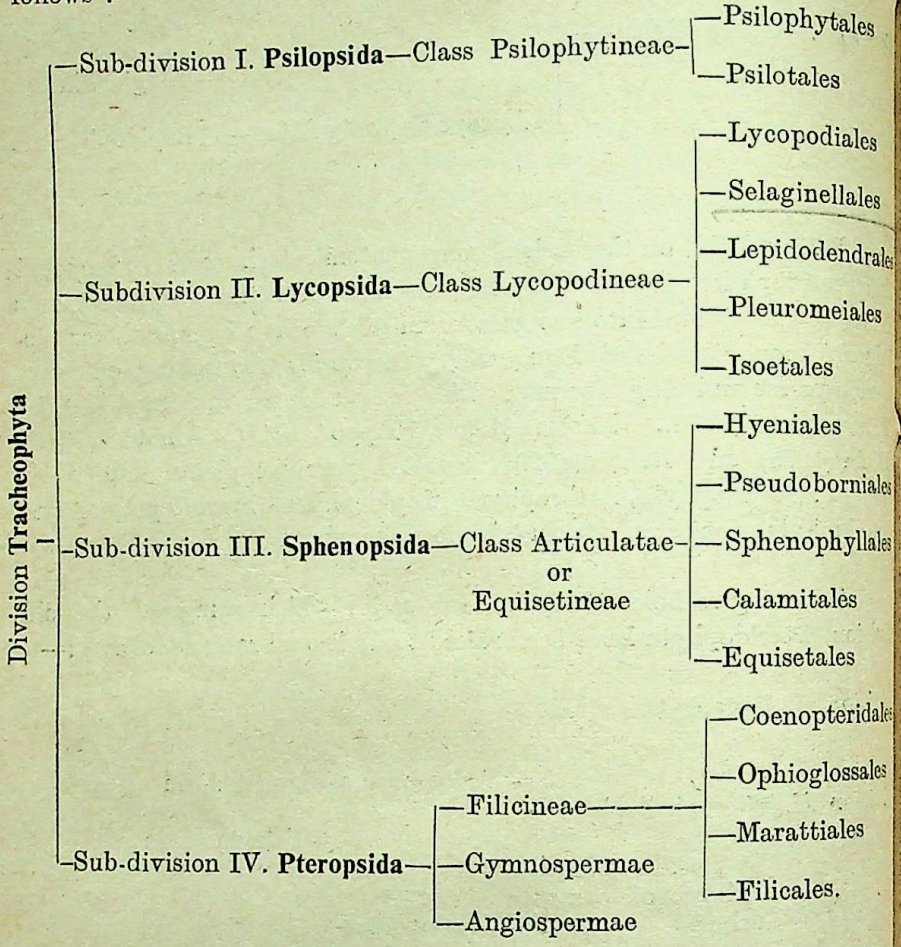
been called Tracheophyta after Sinnot (1935), into four sub-divisions as follows :—



This system best expresses the relationship of extinct plants to the plant kingdom as a whole.

Thus this short review of classification shows how deeply botanists disagree on the classification of Pteridophyta, which is based on fossil plants rather on living ones and since our knowledge about fossil plants is not complete, hence the affinity between the various groups is liable to different interpretations.

Origin of Pteridophyta. Campbell (1895) put forward the theory of the origin of Pteridophytes from Bryophytes. He supposed that the pteridophytean ancestor was a type more or less like the Anthoceropsida. Smith (1938, 1955) supported Campbell's hypothesis. Bower (1935) regards the *"Anthocerotales as a suggestively synthetic Archegoniate type"*. However, this received very little support from later workers. Dr. Rodolfo E. G. Pichi—Sermolli (1959) discards this bryophytean origin.

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Many botanists regard the Algae as the ancestor of the Pteridophytes. Some regard them polyphyletic whereas others support monophyletic origin. Arber (1921) suggested polyphyletic origin of Pteridophytes and maintains that the Sphenopsida, Pteropsida, Lycopsida and Psilotales represent four different lines of descent, each derived from thallophytic algae of distinct type. Gregus (1955) advanced a moderate polyphyletic theory and believed that a part of Psilophytopsida and Lycopsida originated from Chlorophyceae, that a part of Psilophytopsida and Lycopsida, and Psilopsida and Filicopsida derived from the Phaeophyceae, and finally the Sphenopsida originated from the Rhodophyceae through the Characeae. According to Lam (1957), Gregus's phylogenetical ideas are based on an insufficient knowledge of the morphology of living and fossil Cormophyta. Church (1919) in his essay on the "**Thalassiophyta and the subaerial transmigration**" postulates a highly polyphyletic conception of the course of evolution He believes that all the main lines of evolution must have been differentiated in the sea at a very early time from extinct large Sea weeds, called by him the **Thalassiophyta**. He thought that the life of descent of the existing groups of land plants may be traced back to the flagellated organisms of the sea wholly independently of one another. Andrews (1946, 47) supports Church's hypothesis and is of the opinion that they were radiating out in many directions, a few of which became definable as Lycopods, Articulates, Coenopterids etc.

A number of botanists support a monophyletic origin of Pteridophyte from the algae. Schenek (1907) advocated the origin of Bryophyta and Pteridophyta from phaeophyceous forerunners, but this on account of certain evident differences is an unconvincing proposition.

According to Fritsch (1917, 1921, 1945, 1954) the Pteridophytes have originated from Chlorophyceous ancestors such as heterotrichous forms of Chlorophyta, closely resembling the Chetophorales of the present day. Chadefaud (1952) supports Fritsch's views and regards the higher plants as a highly advanced green algae some of rhodomeloid type, others of fucoid type.

Lignier (1911) though supporting monophyletic origin, suggests that the Pteridophytes sprang from a hypothetical group the "**Prolycopodinees**," which were derived from another hypothetical group the "**Prohepaticques**," originating in turn from the algal ancestors, the "**Paracutlerees**," similar to the present Cutleriales (Phaeophyta). Tansley (1907) derives the Pteridophytes from a hypothetical group "**Protopteridophyta**" which had its forerunner in the green algae.

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Bower (1939) criticized the theory of the algal origin of Pteridophyta and said that the Archegoniatae "Stand aloof from any known Thallophytic origin, unless there be some remote connection with Isokont Green Algae. They will be best studied as an independent evolutionary innovation on land, rather than direct extension of a Thallophytic flora from aquatic to sub-acrial habit."

Thus according to Dr. Rodolfo E. G. Pichi-Sermolli (1959) we can conclude that the Pteridophytes have a **monophyletic** origin and derive from ancestors closely resembling the present day Chlorophyta.

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CHAPTER 6

LYCOPODIALES ("The Club Mosses")

This order formed the chief vegetation during the Carboniferous period and was represented by large tree forms, such as *Lepidodendron*, but the present day representatives are all quite small plants, seldom reaching a height of few feet only. Usually they grow in peaty soils on hills, a few grow as epiphytes on tree trunks. The Lycopodiales are distinguished from Selaginellales in having leaves without ligules and homosporous sporangia. The sporophylls may or may not be aggregated to form strobili.

Rothmaler 1954 divided the Lycopodiales into three families :

1. **Urostachaceae**—with a single genus *Huperzia* (Herter's Urostachys)

2. **Lycopodiaceae**—with the genra *Lycopodium, Diphasium, Lepidotis.*

3. **"Phylloglossacees"**—with a monotypic genus *Phylloglossum.*

The order is represented by a single family Lycopodiaceae which has *Lycopodium* and *Phylloglossum* as its representative genera. The former is cosmopolitan in distribution where as the latter is restricted in distribution to parts of Australia and New Zealand. We shall discuss the life history of Lycopodium in detail.

LYCOPODIUM

Systematic position.

Division—*Tracheophyta*

Sub-division—*Lycopsida*

Class—*Lycopodineae*

Order—*Lycopodiales*

Family—*Lycopodiaceae*

Genus—*Lycopodium.*

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Distribution and Occurrence. Lycopodium comprises about 180 species and grows in arctic, temperate and tropical lands (except arid regions) hence world wide in distribution. They are chiefly delicate ever green herbs though shrubby forms like *L. selago* are not uncommon. They are found most commonly on heaths, and on humus soils in moist shady places, especially on hills. They are familiarly known as **"Club mosses", "Ground pines"** or **"Trailing evergreens"** About a dozen species occur in India chiefly in Kashmir, Darjeeling, Nilgiris and Ootacamund. The most common species is *L. clavatum* (Fig. 1)

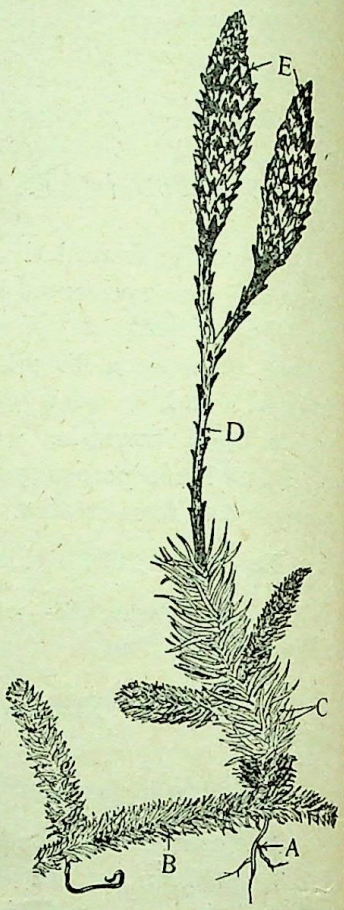

FIG. 1. Habit of *Lycopodium clavatum* showing strobili. *A*, Root; *B*, Stem; *C*, Leaves; *D*, Podia; *E*, Strobili.

External Characters of the Sporophyte :

Stem. The habit of the full grown plant is remarkably different in different species. There are species of Lycopodium with **erect stems** and branches (regarded as sub-genus **Urostachya** by Pritzel 1900) such as *L. selago*, *L aloifolium* and *L. phlegmaria*. On the other hand, many species show **creeping stems** and branches (regarded as a sub-genus **Rhopalostachya** by Pritzel 1900) such as *L. clavatum*, *L. inundatum*, and *L. complanatum*. All of them show that the main stem creeps on, or below the surface of the ground finally becoming horizontal. Many of the tropical species like *L. phlegmaria* with weak pendant branches grow as epiphytes on tree trunks. The branching of the stem is partly monopodial, partly dichotomous, and in most of the cases it is uncertain to say which of the two schemes more properly applies.

Leaves. They are simple, sessile and often narrow elongated (2–10 mm. long). The margin of the leaves may be slightly serrated. The leaf –blade is traversed by an unbranched mid-rib. The stem, in all species, are thickly clothed with such leaves. The leaves vary in form and arrangement. Sometimes, they are whorled, sometimes spiral, or both on the same plant. The whorls may consist of decussate pairs, or be of three, four or more leaves. (Fig. 2). The leaves are all alike in size and shape, but species such as *L. complanum, L. chamaecyparissus* and *L. volubile* possess **dimorphic** leaves like Selaginella arranged in four rows.

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two small, two large on the stem. As the leaves are arranged close to one another in a compact manner so as to cover the stem completely,

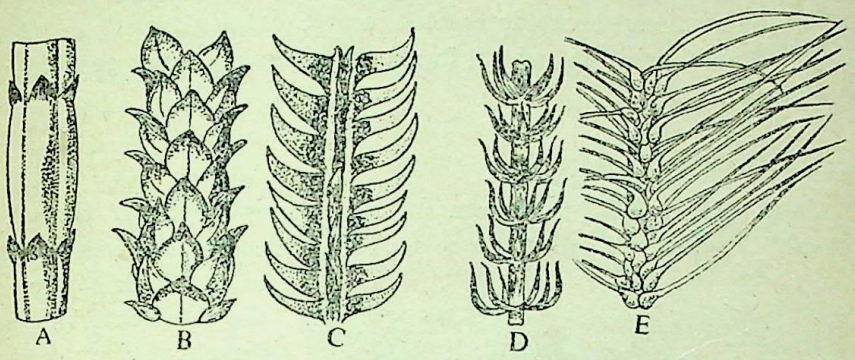

FIG. 2. Shoots of various species of *Lycopodium* to show the form and arrangement of the leaves. *A*, *L. casuarinoides*; *B*, *L. rufescens*; *C*, *L. volubile*; *D*, *L. cernuum*; *E*, *L. mandioccanum*.

there are not only no internodes but the outer layers of cortex of the stem is genetically connected with the tissue of the base of the leaves.

Roots. The first root is short and atleast in some species does not live long. The roots of creeping form are adventitious and arise singly

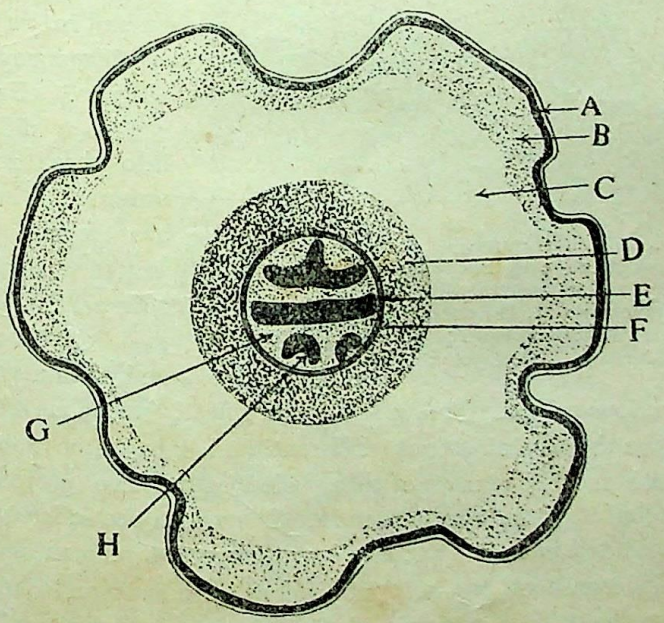

FIG. 3. Diagrammatic T. s. of *Lycopodium clavatum* stem. *A*, Epidermis; B, Sclerenchymatous hypodermis; *C*, Thin walled cortex; *D*, Thick walled cortex; *E*, Endodermis; *F*, Pericycle; *G*, Phloem; *H*. Xylem;

or in groups acropetally all along the under side of the stem. In case

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of erect form (*L. selago* and *L. phlegmaria*) all the roots emerge in a tuft from the base of the enlarged tuberous stems, but these roots according to Strasburger have their origin in as much as 5 cm. inside the tissue of the stem and hence designated as *"Cortical Roots"* or *"Inner Roots"*. Root hairs in terrestrial forms are abundant and persist over a long period.

Internal Structure.

Stem : It is different from all vascular plants. A transverse section of the stem of *L. clavatum* reveals a central **protostele,** surrounded with a thick **cortex,** and the thick cutinised **epidermis**. The central stele is separated from the cortex by **pericycle** composed of from one to three layers of thin walled cells, which are termed as "**phloem sheath**" by Hagelmaier (Fig. 3). The **endodermis** is not well developed and in certain cases is conspicuous by its absence. Usually the cortex is differentiated into three zones. The outer and inner zones are formed of thick walled sclerenchymatous cells, where as the middle zone is composed of thin walled large parenchymatous cells containing few chloroplast. In some cases as in *L. inundatum* the cortex is not differentiated into three zones but is formed of a homogenous mass of thin walled cells. The protostele occupies about half the area of the section. The **xylem** lies in irregular bands and are separated from one another by interspersed phloem bands. The xylem bands consist of tracheids pointed at both ends and increasing in breath from the outside towards the interior *i. e.*, **centripetal** (Fig. 4). The protoxylem, showing spiral and annular tracheids occur at the outer edges of the xylem bands, hence **exarch** in position. The phloem consists of narrow cells. According to Hagelmaier, there occur rows of broader elements in the narrow celled phloem which lie between xylem

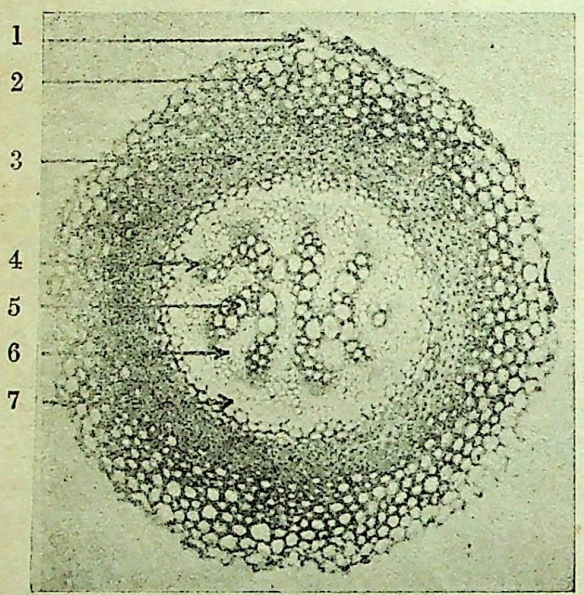

FIG. 4. Photomicrograph of Stem (T. s.) *L. clavatum* showing Plectostelic structure with exarch (external) protoxylems 1, Epidermis; 2, Outer cortex ; 3, Inner cortex; 4, Protoxylem ; 5, Metaxylem; 6, Phloem ; 7, Pericycle ;

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bands. These represent sieve tubes which have no sieve plates. Between the peripheral corners of the xylem bands are bast like fibrous elements, the **"protophloem elements"**. Such a structure reminds us of steler organisation of polyarch roots. Transverse sections at different heights in the same shoots show a different arrangement of xylem and there is wide range of variation in different species.

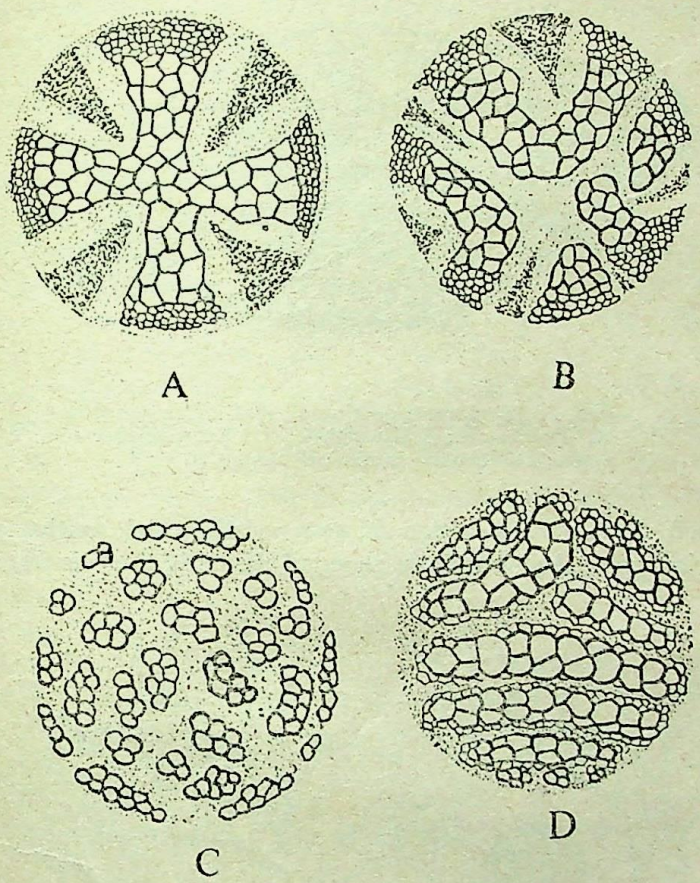

FIG. 5. Diagrammatic transverse-sections of steles of different species of *Lycopodium* showing a wide range in protostelic structure, *A*, Actinostele of *L. serratum*; *B*, *L. annotinum* showing some what stellate arrangement; *C*, Mixed protostele of *L. cernuum*; *D*, Plectostele of *L. volubile*. Dots represent phloem; cells represent xylem.

The simplest structure is represented by *L. selago, L. serratum,* and *L. phlegmaria,* where the xylem-core is star shaped and protoxylem still retains the exarch position. The protoxylem lies in between the xylem bands. Such a protostele is known as **"actinostele"** (Fig. 5A). A slightly evolved arrangement is displayed by *L. volubile*. Here the xylem and phloem in transverse section are arranged in alternate bands running

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parallel to one another designating the protostele as **"plectostele"** (Fig. 5 D). In forms higher than these, such as *L. cernum*, the xylem elements occur as scattered groups embedded in the tissue of phloem, thus showing a **"mixed-protostelic"** structure (Fig. 5C). Only leaf traces are present in such steles, leaf gaps are unkown.

No secondary growth has been seen in any of the species.

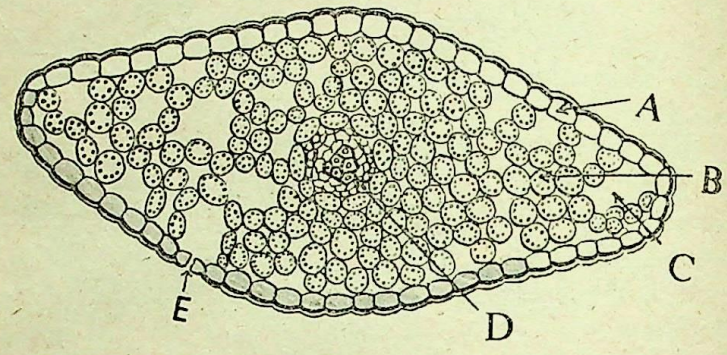

FIG. 6. Transverse section of leaf of *L. clavatum*. *A*, Epidermis; *B*, Mesophyll; *C*, Intercellular air space; *D*, Vascular bundle; *E*, Stoma.

Leaf. A transverse section shows a **midrib**, which consists of a single concentric **amphicribral bundle** (with small xylem in the centre, surrounded by phloem). Xylem is formed of thick walled annular and spiral

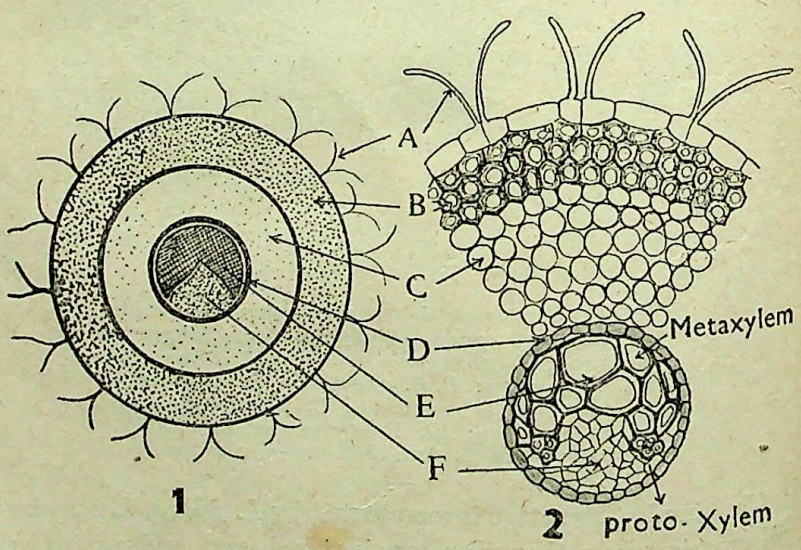

FIG. 7. *L. pithyoides*. T. s. of cortical root; *1*, Diagrammatic section; *2*, Detailed structure; A, Epidermal hair; *B*, Scle hypodermis; *C*, cortex; *D*, Endodermis; *E*, Xylem; *F*, Phloem.

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tracheids and phloem is composed of narrow sieve tubes and phloem parenchyma. The mid-rib bundle is surrounded by sclerenchymatous **pericycle**. The **endodermis** can hardly be recognized. The leaf is bounded by a highly cuticularized **epidermis** (Fig. 6). The epidermis in the leaves of *L. annotinum, L. clavatum, and L. selago* has stomata on both surfaces but those of heterophyllous species with four rows of two small and two large leaves have stomata only on the lower surface. The **mesophyll** tissue fills the space between the epidermis and midrib and is not differentiated into spongy and palisade cells.

Roots. The root in transverse section shows a circular outline (Fig. 7). The outermost layer is thin-walled **epidermis**, from which unicellular **root-hair** arise. The root-hair are anomalous in that they develop in pairs. Below it, lies a broad cortex, divisible into an outer sclerenchymatous **hypodermis** and an inner thin walled parenchymatous region. The thin roots reveal a **monarch** structure but thick ones like that of *L. clavatum* and others show a complex structure approaching very near to that of the stem. The only difference being that the stele of roots is smaller and simpler and that leaf traces are only confined to stem. There are from 7-10 protoxylems and the corresponding metaxylem masses usually unite in the centre revealing a stellate form, with phloem tissue between the rays. **Diarch roots,** with horseshoe or crescent shaped xylem and a single mass of phloem with the protoxylem points confined to the tips, are seen in certain species like *L. selago, L pithiyoides* etc.

Lycopodium can easily be regarded as a "**curiosity of nature**" in that the stem and root display the same anatomical structure. The similarity indicates the unity of the axis in all its parts whether leaf bearing or not.

Vegetative Propagation. Besides fragmentation, it occurs by several means as follows :—

1. **Adventitious buds.** According to Strasburger these develop at the base of the stem, as in *L. aloifolium, L. reflexum* and others and are capable of developing new plants when detached.

2. **Bulbils.** These may develop in tropical epiphytic plants or in erect forms from roots or leaves or from the fragment of the plant and grow directly into new plants. Smith (1920) regards them as modified leaf, though some prefer to call them as modified sporangia and modified lateral branches.

3. **Death and decay** of older portion of the branches so that the young dichotomous branches survive as individual plants.

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4. Gemmae. According to Hagelmaier these are branches of peculiar kind and are formed annually on new stem tips in place of a leaf as in *L. selago*, *L. lucidulum* and *L. phlegmaria*. These gemmae have few leaves and a rudimentary root. They are shortly stalked pear-shaped bodies and develop in clusters. Since they are provided with stored food material they tide over the unfavourable period (Fig. 8). When detached, the gemmae are capable of producing new plants. Smith (1955) regards them to be developed from cortical cells of the root.

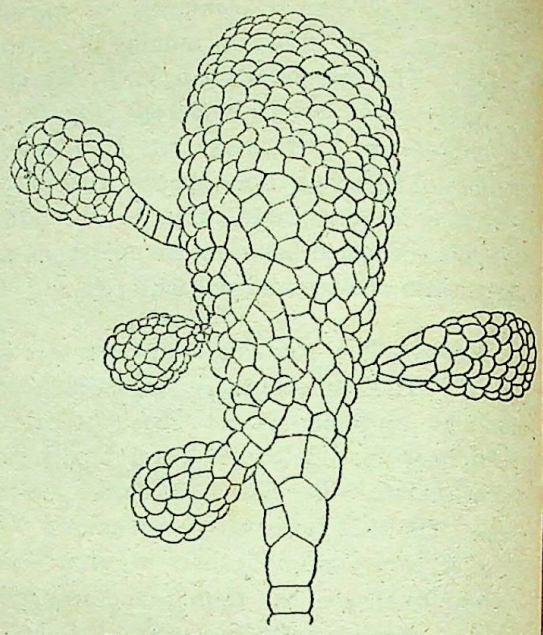

FIG. 8. Gemma with secondary gemmae of *Lycopodium*.

5. Resting buds. These develop during the winter in *L. inundatum* where entire plant, except the tip of the rhizome dies. This tip behaves as a resting bud and on return of favourable season unfolds itself into a new plant.

6. Tubers. These are developed at the apices of the roots and are capable of germinating new plants.

Reproduction. The fertile region, in majority of cases, and in creeping species is represented by **strobili** which are borne in pairs at the apices of erect elongated stalk like branches, the **podia** (Fig. 1). These are sparcely covered with minute scale leaves. The strobilus is made up of a **central axis** on which are closely arranged a large number of acutely pointed **sporophylls**. The **sporangia** are borne singly, close to the base, on the upper surface of the sporophylls (Fig. 9). The sporo-

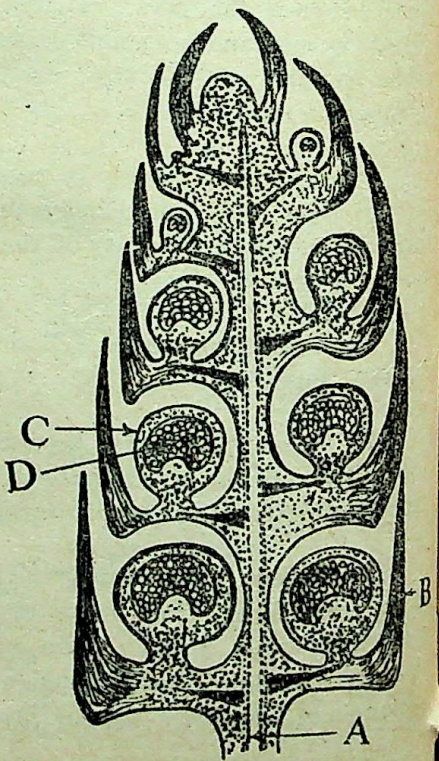

FIG. 9. L. S. of *Lycopodium* Strobilus tip. *A*, Axis ; *B*, Sporophyll, *C*, Sporangium; *D*, Spores.

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pyhlls differ a great deal in various species. Either they are like the sterile leaves or are somewhat smaller in size *e. g. L. lucidulum.* According to Smith (1955) the sporophylls in *L. selago* are borne in series alternating with series of foliage leaves. Such species are considered primitive, whereas those bearing strobili are regarded as most advanced.

Sporangia. The large yellow sporangia are borne singly, close to the base, on the upper (ventral) surface of the sporophylls. All the sporangia are alike. They are non-septate sacs more or less reniform, having a short broad stalk, and a large number of spores. (Fig. 10).

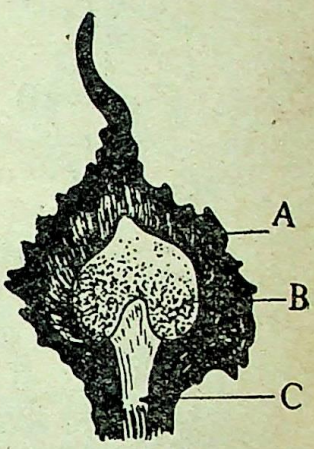

FIG. 10. Sporophyll of *Lycopodium*. *A*, Sporophyll; *B*, Sporangium, *C*, Stalk.

Development of sporangia. The development of sporangia is of **eusporangiate** type. The sporangia develop from a transverse row of superficial cells. These divide to form three layered thick **wall,** the inner most layer of this forms a nourishing layer for the spores, the **tapetum** (Fig. 11). The central **archesporium** consists of three tangential rows of twelve cells each, which by division, produce **spore-mother-cells.** These divide meiotically producing tetrad of **spores.**

Dehiscence. When mature the sporangia may reach a diameter of 1 to 2.5 mm. The sporangium opens by a slit which runs in the direction transverse to the median plane of the leaves and divides the sporangium into two valves which remain united at the base thus scattering the yellow spores. At this stage, the tapetum collapses. In species with compact strobili, this is preceded by slight elongation of the internodes, and by drying and spreading of the sporophylls.

Spores. The production of spores marks the end of diploid sporophytic generation and the beginning of haploid gametophyte. The small spores are between round and tetra hedral in form. They are produced in large number and are **uniform** in size and shape *i. e.*, **homosporous.** The spores are light with thin exine and intine aud contain chloroplast in small amount. The exine shows a variety of markings on it.

Germination of Spore And Development of Gemetophyte (prothallus). The germination shows a wide range of variation. According to Treub (1888) the germination may take place within a few days after they are

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shed *e. g.*, *L. cernum* and the gametophyte is cylindrical and short lived. But Bruchman (1910) is of the opinion that usually it is slow and takes

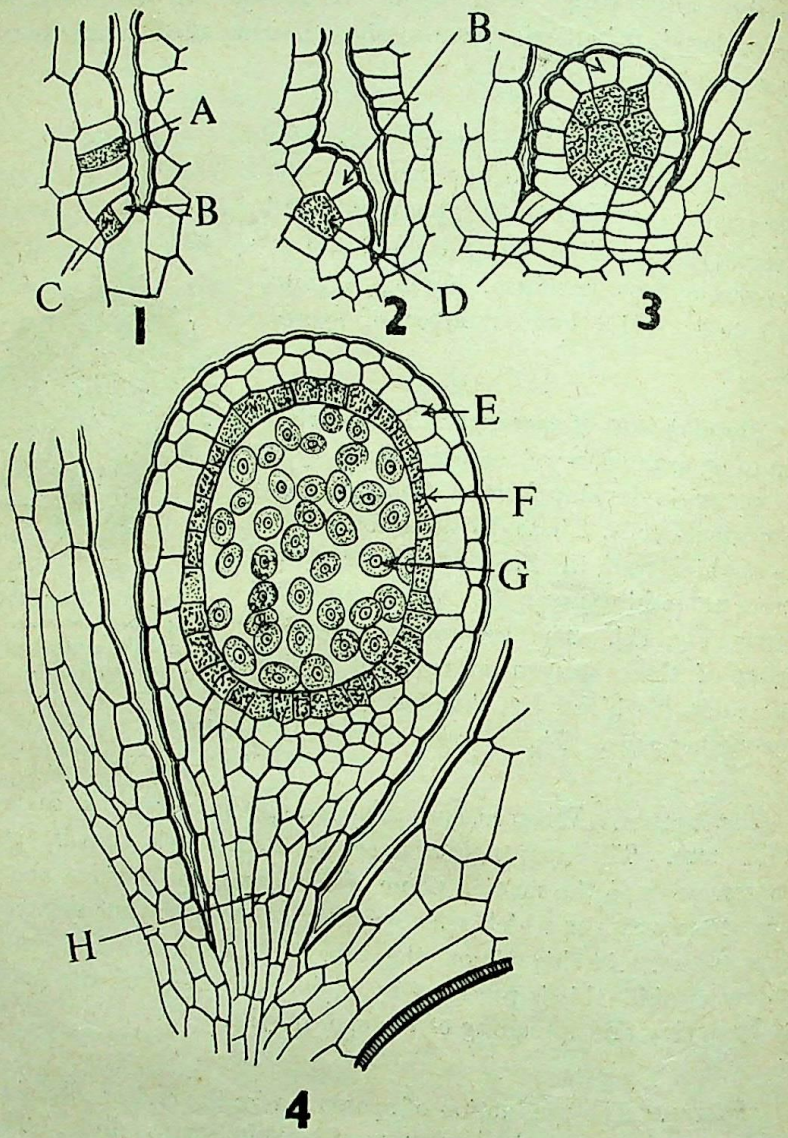

FIG. 11. Development of sporangium of *Lycopodium* (1—4), 1, Young sporophyll showing a sporangial initial (*A*) and its division into jacket initial (*B*) and archesporial initial (*C*); *2*,—*3*, Later stages; *4*, L. s. of older sporangium showing sporangiwal wall (E), tapetum (*F*) spore-mother-cells (*G*), and stalk (*H*).

about three to eight years though in certain cases that have a colourless subterranean gametophyte nourished by a **symbiotic mycorrhiza** it may take even fifteen years to mature. So far as this germination is concerned, it has not been duplicated by any of the ferns.

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We owe to de-Bary (1858) who has succeeded in seeing the first stages in the development of the prothallium of *L. inundatum*. During the germination of spores, the **exine** opens by three valves and **intine** comes out in the form of a spherical vesicle Fig. 12. This divides in a trans-

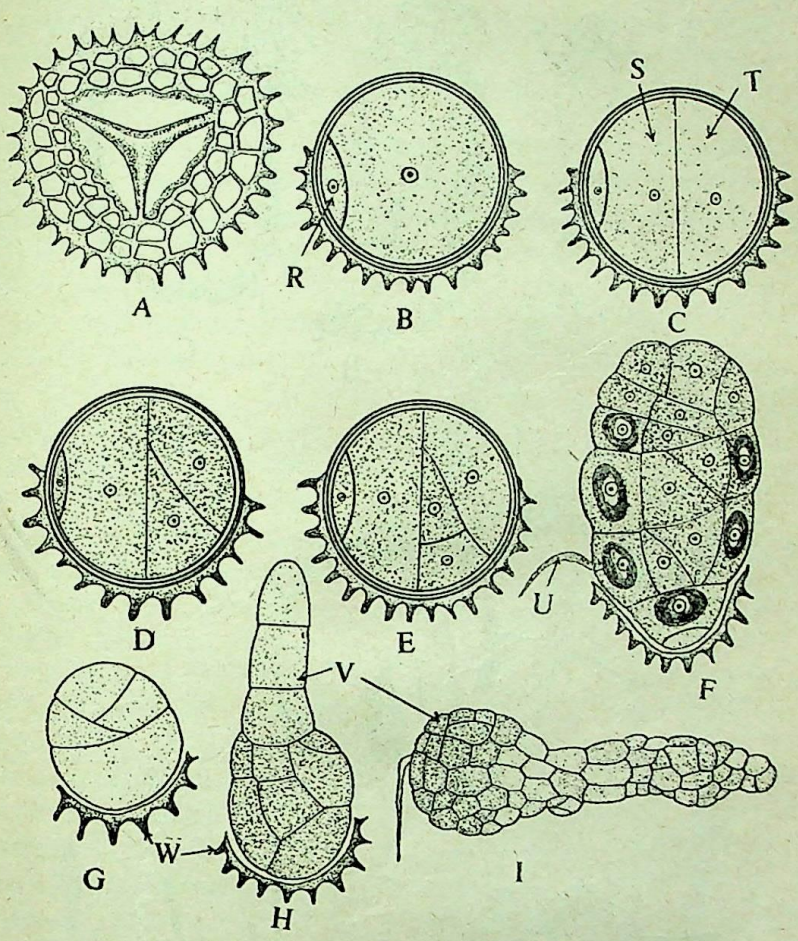

FIG. 12. Spore and development of gametophyte of *Lycopodium*. *A*, spore; *B*,—E, Early stages of the development of gametophyte; *F*, Gametophyte of L. annotinum showing mycorhiza ; *G*—*I*, Early development in *L. cernuum*. (*U*, Fungal hypha. *V*, Primary tubercle ; *W*, spore wall; *Q*, Rhizoidal cell; *S*, Basal cell, *T*, Apical cell).

verse wall into an inner basal cell which suffers no further change except cutting of a small lens shaped **rhizoidal cell** (Fig. 12B) and an outer cell which develops as an **apical cell** and formed two rows of segments. Further development of this 4—5 celled gametophyte is arrested unless and until the hyphae of a symboitic phycomycetous fungus enter the basal cell forming mycorrhizal association (Fig. 12 F). When the fungus has entered the basal cell, the apical cell cuts off about six segments which develop a group of meristematic cells. Each segment is divided by a periclinal wall into an inner and outer cell. The latter gets infected with symbiotic

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fungus. From the apical group of these cells arise a major portion of the adult gametophyte, which shows great diversity in form and structure.

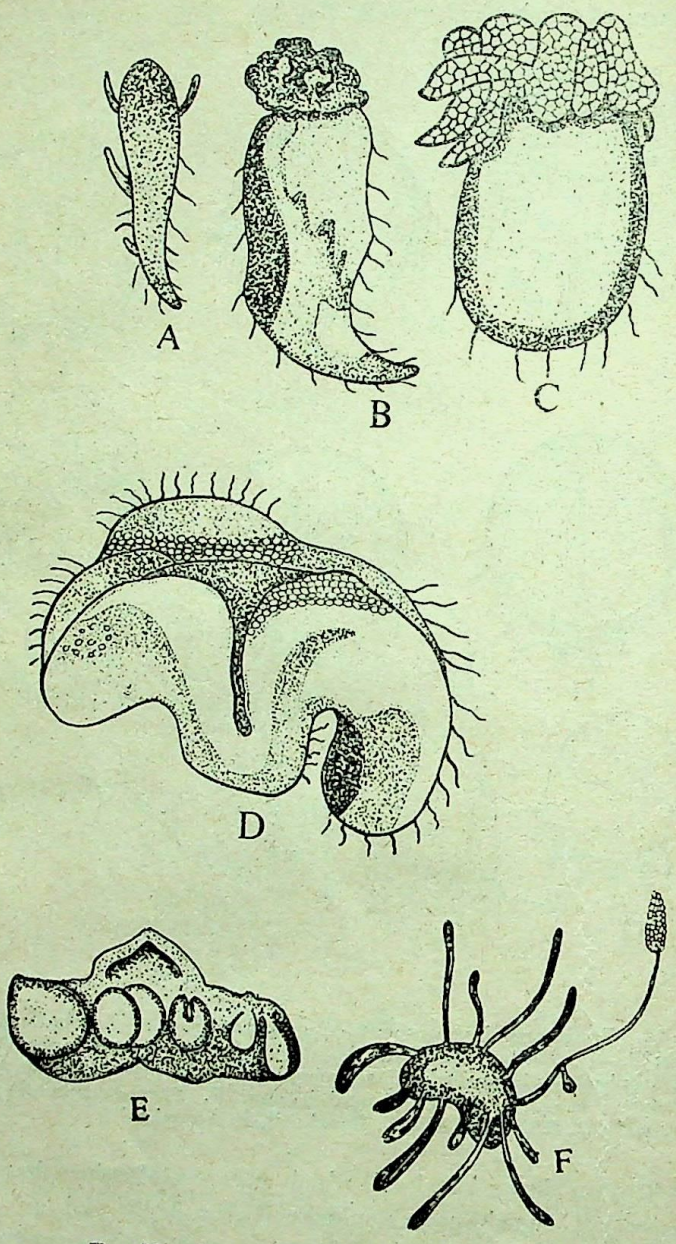

FIG. 13. Gametophytes of various species of *Lycopodium*. *A*, *L. selago* : *B*, *L. complanatum* ; *C*, *L. cernuum*; *D*, *L. clavatum* *E*, *L. annotinum* ; *F*, *phlegmaria*.

The mature prothalli. According to Treub (1889) and Bruchman (1916) the prothalli of this genus are distinguished into a number of types as follows (Fig. 13).

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(I) In the first type as seen in *L. cernuum*, *L. obscurum* and *L. complanatum*, the gametophyte is an **up-right fleshy structure** whose lower portion is embedded in the soil (Fig. 13 B, C). On its upper part develop green lobes with meristematic strands. The sex organs are developed at the base of these lobes. In spite of the constant pressure of the symbiotic mycorrhizal fungus, the prothallus is autophytic. The pressure of the fungus makes it partially saprophytic.

(II) The second type is seen in species such as *L. clavatum*, *L. annotinum* and *L. camplanatum* where the large prothalli are **completely subterranean, tuberous, non-green, without lobes, and incompletely saprophytic,** (Fig. 13 D, E) The sexual organs develop on the hollow (cup like) upper surface. Here the nutrition is entirely saprophytic.

(III) In the third type e. g., in epiphytic species like *L. phlegmaria* where the large saprophytic prothalli are **attenuated in form and branch monopodially** into colourless cylindrical branches, which may become independent as a result of a apical growth and posterior decay (Fig. 13 F). The sexual organs are developed on the upper surface of the enlarged branches. The presence of the paraphyses is an anomalous feature.

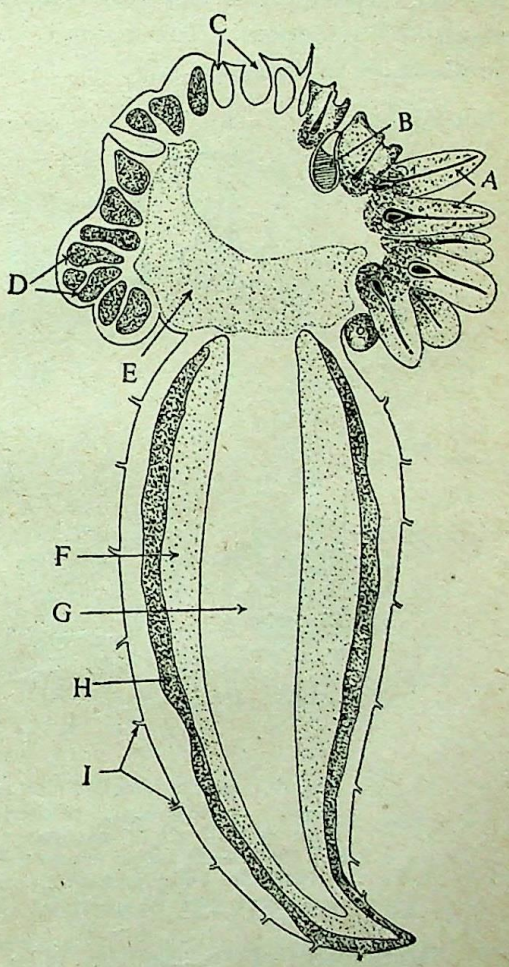

FIG. 14. Diagrammatic Median Vertical section of the prothallus of *L. complanatum*. *A*, Archegonia; *B*, Embryo; *C*, Empty antheridia; *D*, Antheridia; E, Meristematic collar; *F*, storage tissue; *G*, Pith like region; *H*, Mycorhizal zone ; *I*, Rhizoids.

On the basis of the wide diversity which the prothalli of *Lycopodium* show, there is a tendency now-a-days to revive the ideas of Dillenius (1741) and Palisot de Beauvois (1805), and to split it into two or more genera. Herter (1922) sub-divided Lycopodium into two genera **Urostachys** and **Lycopodium**. The former is known by various names by different workers : (*Selago* Boehm; *Mirmau* Adans, *Huperzia* Bernh, *Plananthus*

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Pal, Beauv) Rodolfo E. G. Pichi-Sermolli (1959) prefers splitting the genus into **Huperzia** and **Lycopodium,** we eagerly await the contribution of other workers in this direction.

A transverse section of the prothallus of *L. complanatum* reveals that it is bounded by an outer **epidermis** which is followed by a multi-layered **cortex,** in side which lies the **symbiotic mycorrhizal fungus** forming a hyphal tissue. This is followed by a single layer of elongated **palisade** cells, which in turn is followed by a central **storage tissue** of hexagonal cells. Unicellular rhizoides are given off in the under ground portion. The upper surface shows **antheridia** and **archegonia** in various stages of development. This region is known as **generative tissue.** The prothalli are monoecious.

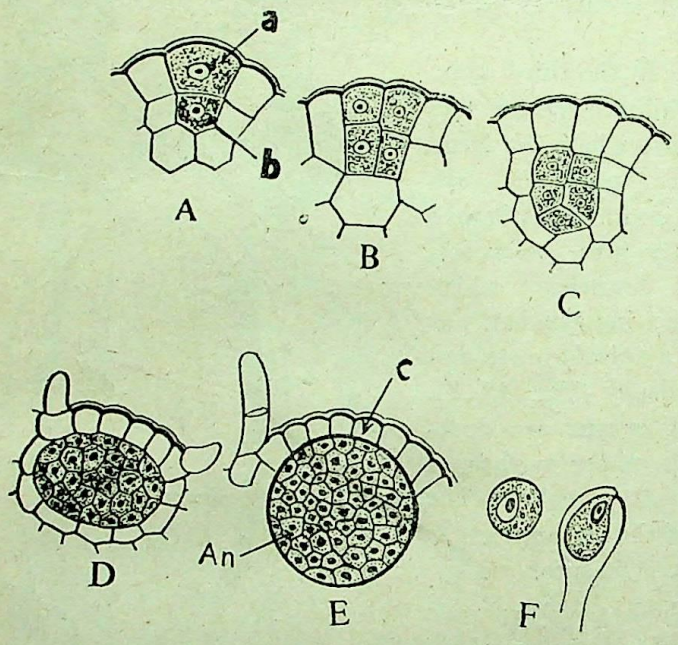

FIG. 15. Development of Antheridium of *Lycopodium* A—E. *A*, Division of antheridial initial into outer primary wall cell (*a*) and inner primary androgonial cell (*b*), *B—D*, Later stages ; *E*, Mature antheridium showing an outer jacket (*c*) and a central mass of androcytes (An) *F*, sperms.

Development of Antheridium. The antheridium initial is an epidermal cell of the prothallus just behind the apical meristem and it developes an antheridium. This cell divides periclinally into an inner **androgonial initial** and an outer **jacket initial.** The latter divides anticlinally to form an outer **jacket layer,** one cell in thickness, whereas the former undergoes a number of divisions to form a large number of **sperm-mother-cells** which are surrounded by the jacket layer (Fig 15).

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The **sperms** are biciliate and fusiform and are similar to those of Bryophytes. When mature a triangular **opercular cell** or a few jacket cells become mucilagenous. This results in the absorption of water which causes the dehiscence of the antheridium thus liberating the biciliate sperms.

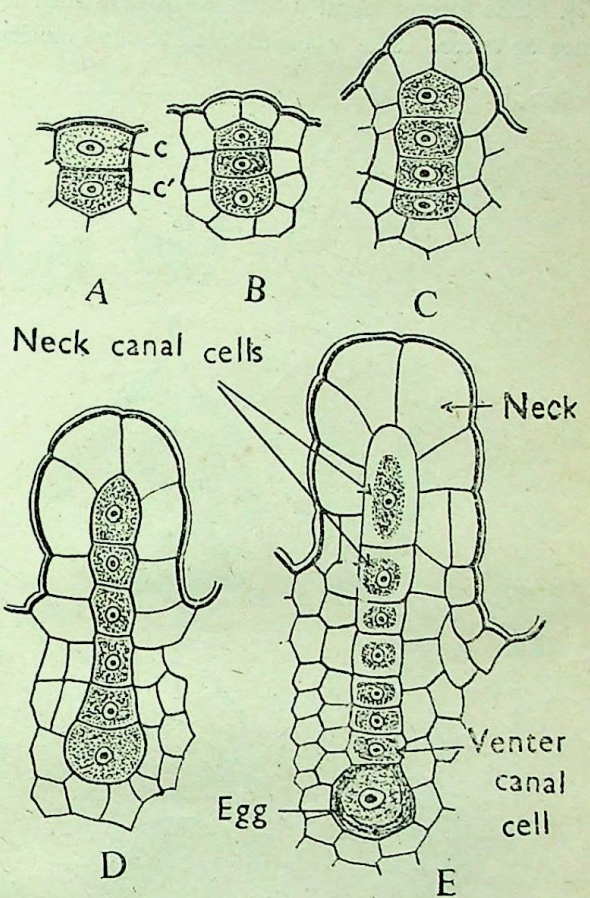

FIG. 16. Development of archegonium of *Lycopodium* (A—E) *A*, Division of archegonial initial into an outer cover cell (*C*) and an inner central cell (*C*); B—D Later stages; E, Mature archegonium.

Development of the Archegonium. The development of the archegonium may be traced to single superficial cells (Fig. 16) The **archegonial initial** divides periclinally into an outer **cover cell** and an inner **central cell** (Fig. 16 A). The former divides anticlinally to form four **neck initials** which undergo transverse division to form a long and straight **neck,** 3–4 cells in height and composed of four vertical rows of cells. The latter undergoes a periclinal division to form a **primary-canal-cell** and a **primary-ventral-cell** (Fig. 16 B and C). The former divides transversely to form about six neck-canal-cells, whereas the latter directly behaves as an **oosphere.** (Fig. 16 D, E).

Fertilization. When mature, the neck cells separate, the neck canal-cells disorganise forming a mucilagenous product which draws the biciliate sperms to the orifice of the archegonium. A number of sperms enter the neck but only one fuses with the oosphere to form an **oospore.**

Development of Embryo. The fertilised egg soon secrets a wall and behaves as a **zygote.** The whole process of the development of the embryo is extra-ordinarily slow, so much so that the young sporophyte takes several years before reaching the surface of the soil. According

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to Bruchman (1910) the first division of the zygote is always transverse and separates an upper **suspensor cell** and the lower **embryonic cell** (Fig. 17). The former usually does not divide and if it does, it may divide once or twice. The latter divides thrice vertically and transversally to

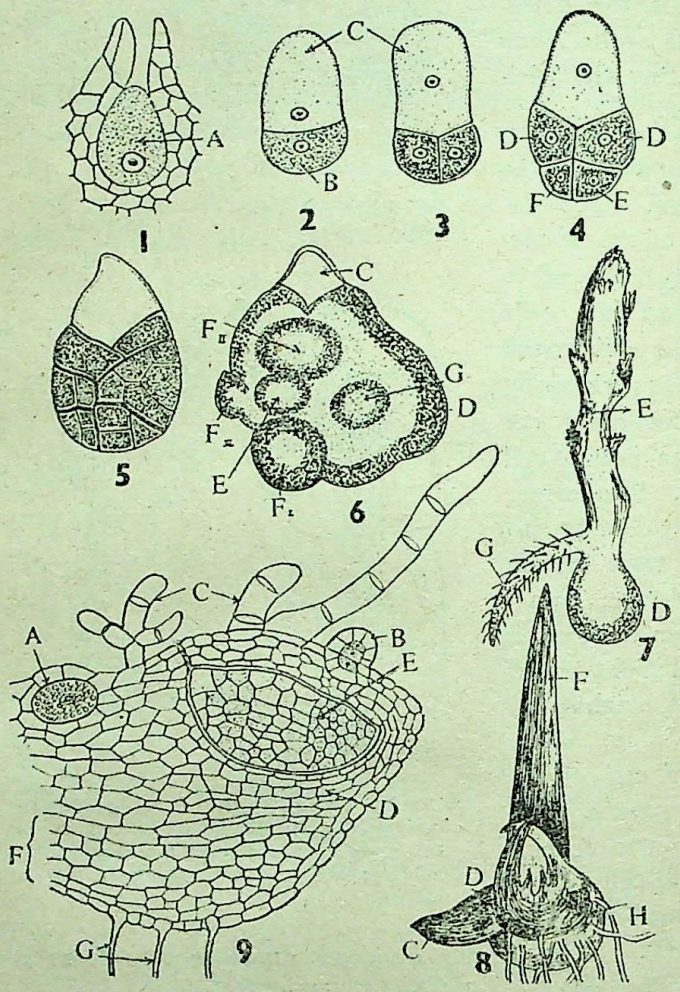

FIG. 17. Development of embryo of *Lycopodium* 1—7. 1, Zygote (*A*); *2—3*, Division of zygote into an embryonal cell (*B*) and suspensor cell (*C*); *4*, Differentiation of the cells of embryo into foot (*D*), stem (E) and leaf (*F*); *5*, Later stage; 6, View of embryo from above showing origin of 3 leaves (FI, FII, FIII) stem apex (E), foot *D*, and root apex (G); *7*, Young plant with foot, stem and reduced leaves; *8*, Embryo of *L. cernuum* showing protocorm (*H*); *9*, Median longitudinal section through a strong archegonial end of the thallus of L. Selago showing an embryo; [(*A*) Antheridium; (*B*) Archegonium; (*C*) Paraphysis; (*D*) Meristem; (E) Embryo; (*F*) Fungal region; (*G*) Rhizoids.]

form a spherical group of eight cells, arranged in two superimposed tiers of four cells each, forming the **octant stage** of the embryo. From the lower tier, two cells form the **stem** and two form the **first leaf** and **primary root**. The upper tier branches obliquely forming a **tuberous foot**, which serves

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as an intra-prothalial haustorium for deriving food from the prothallus until the embryo leads an independent life. The first root shows an

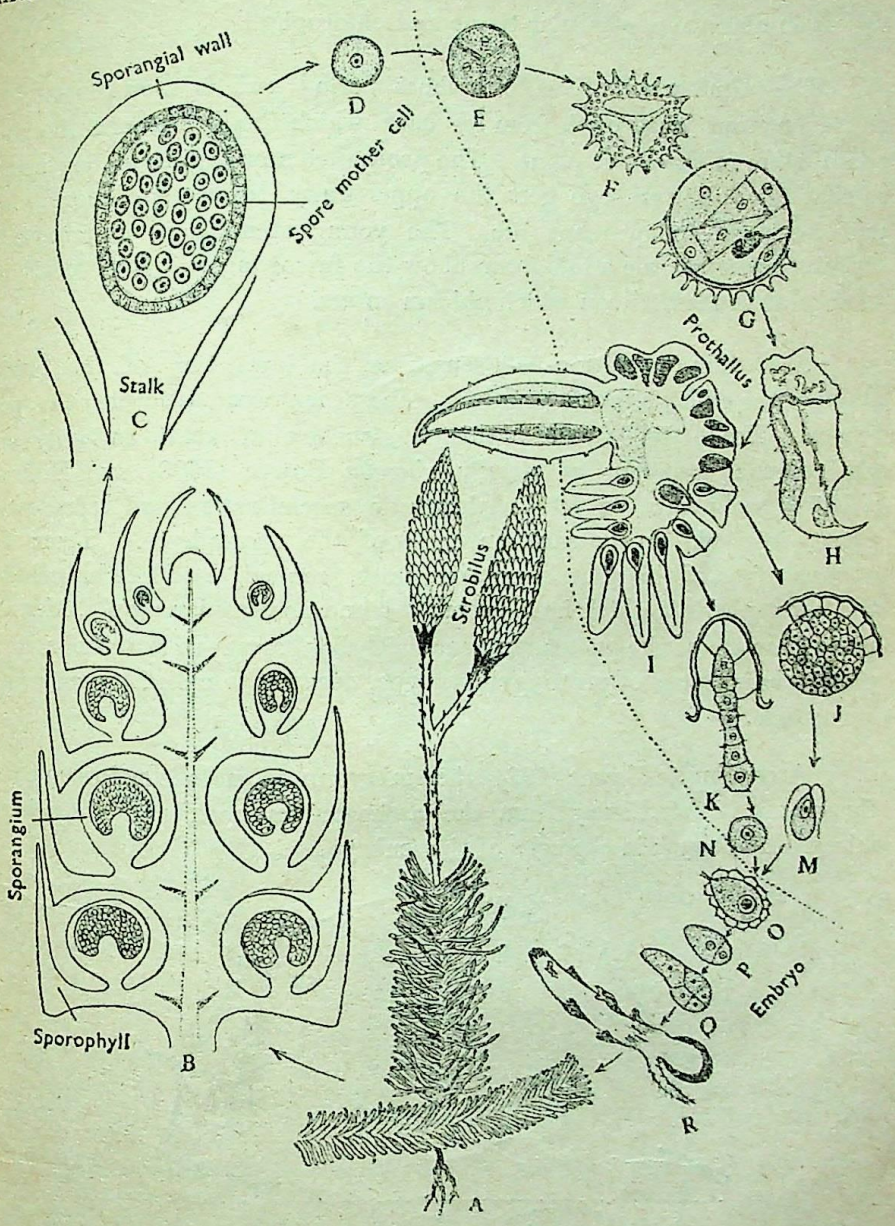

FIG. 18. Diagrammatic representation of the life history of *Lycopodium* [*A*, Sporophytic plant; *B*, L. s. of Sporangium; *C*, A single sporangium having 2x spore mother cells; *D*, A single spore mother cell; *E*, Tetrad of spores (x); *F*, A single spore; *G*, A germinating spore with mycorhizal association; *H*, Gametophytic prothallus; *I*, L. s. of prothallus showing antheridia and archegonic; *J*, An Antheridium; *K*, An archegonium; *M*, Sperm; *N*, Egg; *O*, Zygote (2*x*); *P*—Q. Development of embryo; *R*, young sporophyte.]

exogenous development though subsequent roots are endogenous in developed and have been called "**cladogenous**". As the stem grows, it

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emerges from the prothallus and develops more leaves on it. The first leaves differ from those on the mature plants in their scale like habit as well as in absence of vascular tissue and chlorophyll.

The primary stem lives for a short period and is soon replaced by an adventitous outgrowth from its base which finally becomes the horizontal stem of the adult plant. The prothallus now begins to degenerate so that the young embryo gets the opportunity to develop more roots and leads an independent life. The young stem shows a **protostelic** structure whereas the adult forms show the furrowing of xylem mass into several bands between which phloem enters.

According to Smith (1955) sometimes the lower tier of the octant stage of the embryo develops into a globose massive structure the **protocorm**. Treub (1890) regards this "**a structure of great antiquity** and **phylogenetic precursor of stem**", whereas Bower (1908) and Hollway (1910) regards this, "**a late phylogenetic specialization and represents a "gouty interlude**" in the early ontogeny of the sporophyte. From the upper surface of this protocorm arise erect, conical, leaf-like branches—the "**protophylls**", which have no mid-rib and no vascular supply. Mention must be made of the australian genus *Phylloglossum* where the mature plants show leaves of protophyllous type, hence it is called "**permanently embryonic.**"

According to Bower (1934) the embryo in all cases is **endoscopic** *i.e.*, the apex is directed away from the archegonium neck and there is no micorrhizal fungus in the cells of the embryo.

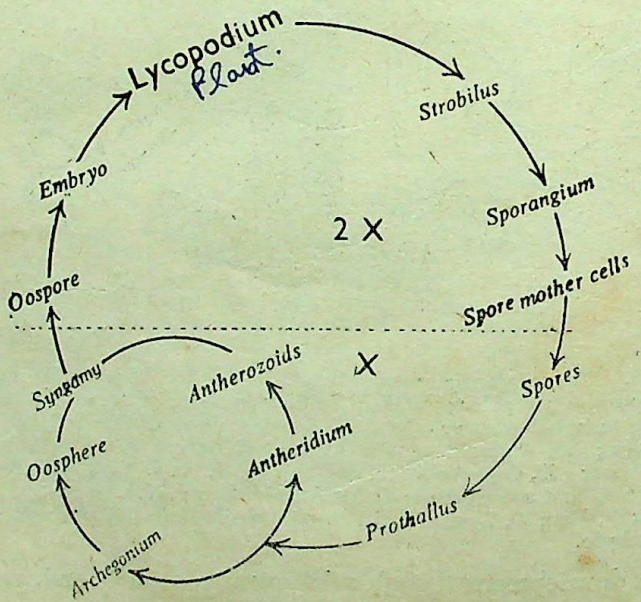

FIG. 19. Life cycle of *Lycopodium*

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shaded habitats of hills. During the dry period the plant rolls up into a compact ball and may tide over the unfavourable period, but resumes the normal activity when moist *e. g. S. lepidophylla* and *S. rupestris*. These plants are called **"resurrection plants"** and are often sold as a novelty (Fig. 20). *S. oregana* is an epiphytic species which grows on the branches and trunks of moss covered trees. The plants are perennial though delicate annual forms are not uncommon *e. g. S. pygmaea and S. gracillima*. About 58 species have been reported in our country from Himalayas and hills of the South India. The common Indian species are *S. kraussiana, S. crysocaulos, S. chrysorrhizos, S. pallidissima, S. sanguinolenta*, and *S. jacquemonth*.

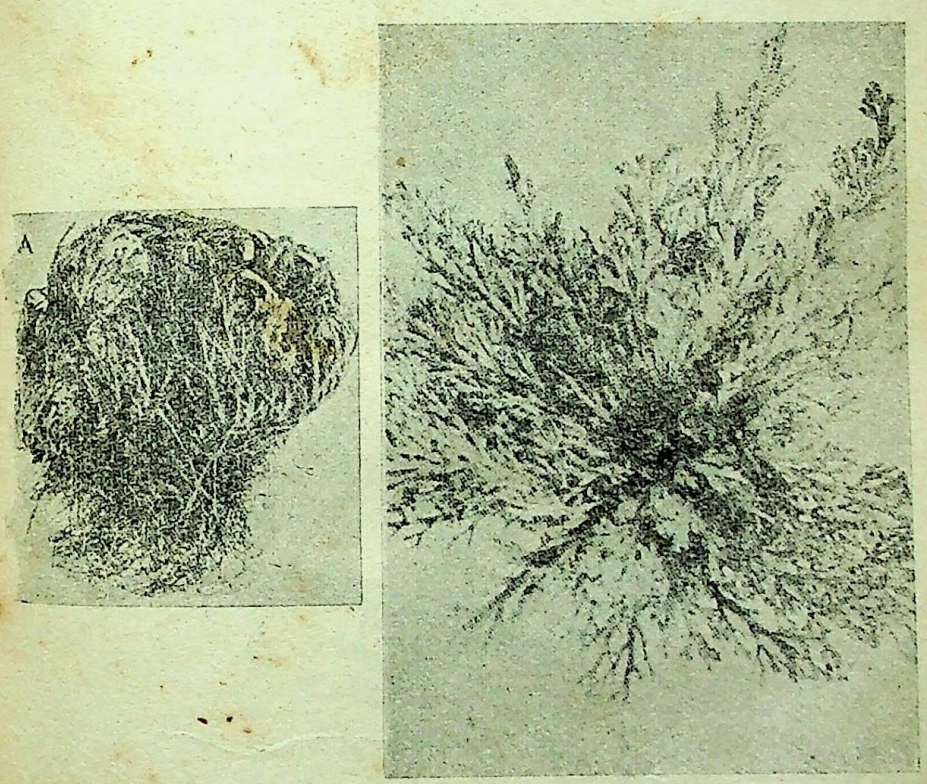

FIG 20. *Selaginella lepidophylla* "The resurrection plant". *A*, Dry *B*, Moistened.

External characters of the Sporophyte. The plant is sporophyte and is evergreen delicate herb with adventitious roots. In some species the branching stem is **prostrate** growing along the surface of the ground, *e. g., S. krauassiana* or may be **sub-erect**, *e. g., S. trachyphylla* or may be **scandent** as in *S. wiledenovii*. The stem is covered with four rows of small leaves. Out of these, two rows are of smaller leaves and two of large leaves. The species with **dimorphic** leaves were grouped by Hieronymus (1900) in the sub-genera **Heterophyllum**. In other species the stem may be **erect** with a spreading

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mass of foliage uniform in size *e. g.*, *S. spinulosa, S. oregana,* and *S. selaginoides*. Such species with uniform leaves were grouped in the sub-gebera **Homoeophyllum**. The stem covered with these green leaves presents a moss like appearance, hence the plant is called "**little club moss**" (Fig. 20.)

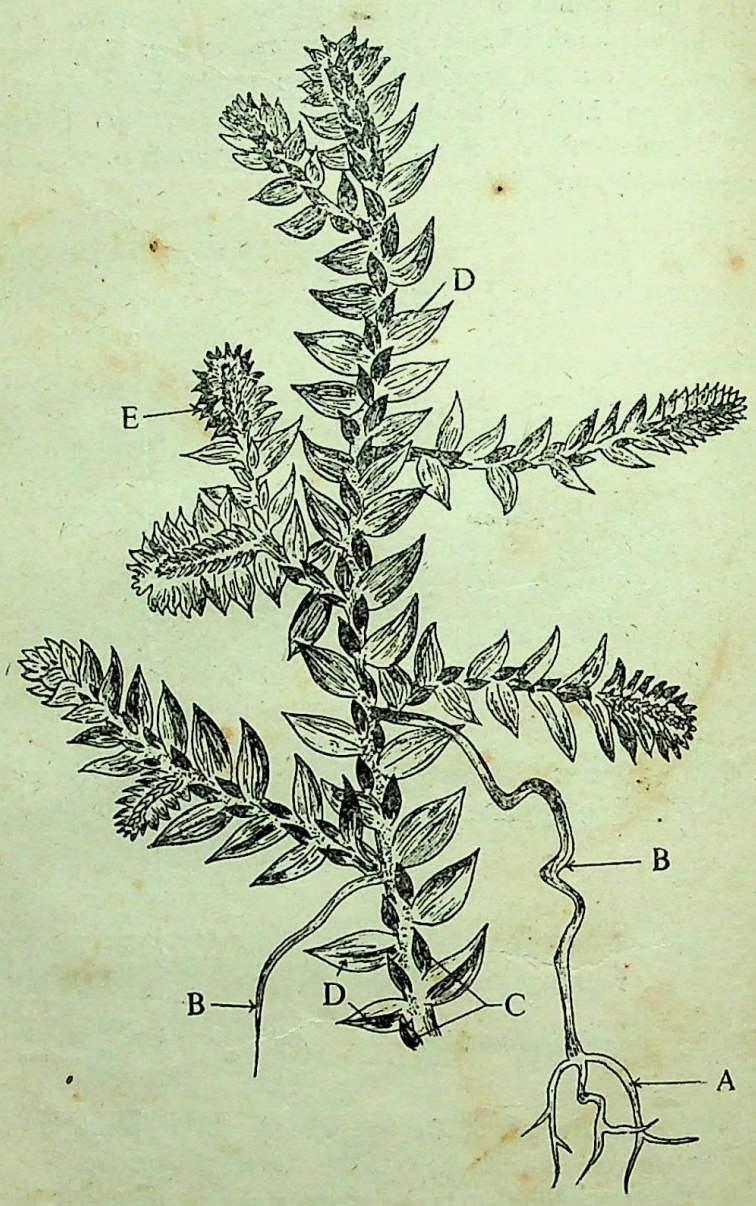

FIG. 20. Habit of *Selaginella kraussiana* ; *A*, Root ; B, Rhizophore ; *C*, smaller leaves ; *D*, Larger leaves; E, Strobilus.

The **leaves** are in pairs and are conspicuously **different** in size. The **small** leaf of each pair is inserted on the dorsal side of the stem and the **larger** on the ventral side. Successive pairs of leaves are so arranged

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a thick walled hypodermis and certain stetar peculiarities. In *S.*

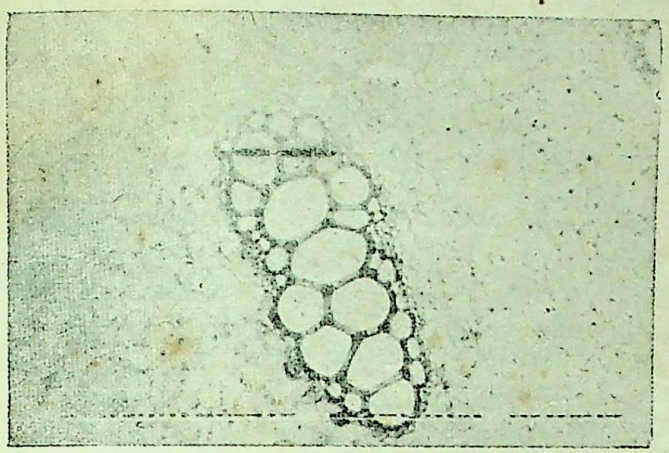

FIG. 23 II. Photomicrograph of a xerophytic species showing stele Note the trabeculae are conspicuous by their absence.

kraussiana, *S. poulteri* and *S. delicatissima*, the protoxylem lies in the centre *i. e.* **centroxylic** or it may be in the form of a number of strands situated in the cresentric metaxylem as in *S. atrovirdis* (Fig. 26).

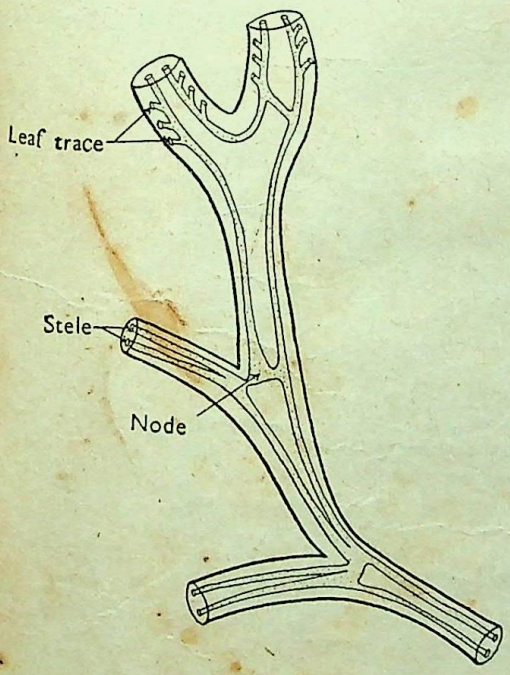

FIG. 24. Diagrammatic view of *Selaginella kraussiana* stem showing bifurcation of the stele at the branch nodes. Leaftraces have only been shown at the top.

The morphological nature of rhizophore has long been a puzzle. The following are the three important views which have been advanced from time to time to prove its possible nature : (1) According to Gibson, Van Tieghem (1902) and Uphof (1920) the rhizophore is regarded as a **capless root** and resembles it so far as positive geotropic nature and leafless form is concerned. (2) Treub, Pfeffer, Bruchmann and Troll regard it as a **leafless shoot** due to the absence of root-cap, root hairs and their formation from angle meristem giving a dichotomous nature to the stem. (3) Williams (1938), Goebel and Bower regard this as an **intermediate structure** between root and shoot and hence an "**organ suigeneris**".

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Structure of leaf. The leaf displays a simple structure. The cells of the upper and lower **epidermis** contain chloroplasts. The **stomata**

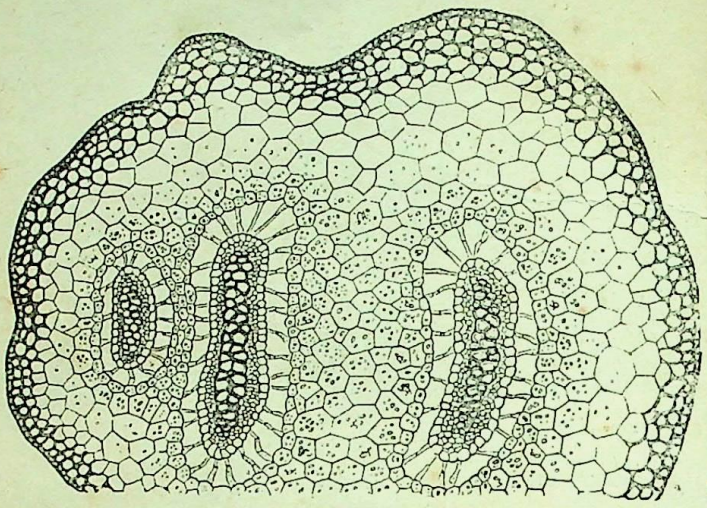

FIG. 25. T. s. of a polystelic stem of *Selaginella.*

are present near the mid-rib only on the lower epidermis. On the sides

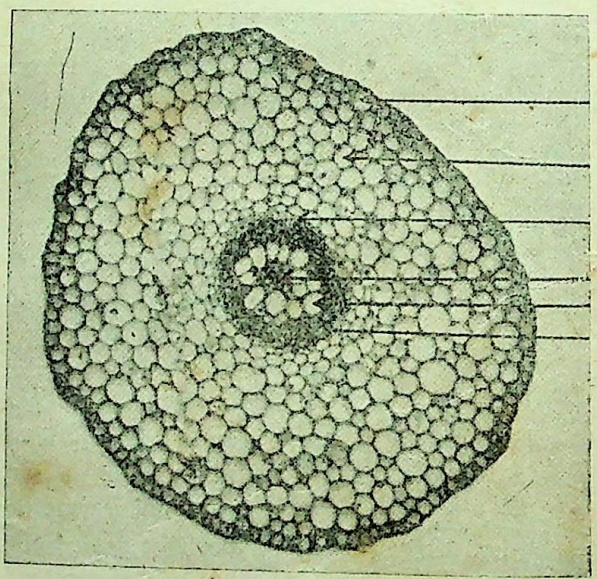

FIG. 26. Photomicrograph of the T. s. of the rhizophore of *S. kraussiana.* Note the simple concentric stele with internal centroxylic protoxylem. 1, Epidermis; 2, Cortex; 3, Endodermis; 4, Protoxylem; 5, Metaxylem; 6, Phloem.

there is loose spongy **mesophyll**. Generally the mesophyll is not differentiated into palisade and spongy parenchyma except in *S. lyalli.* where a well developed palisade parenchyma is developed. In the centre lies a single concentric **amphicribral bundle** (Fig. 27).

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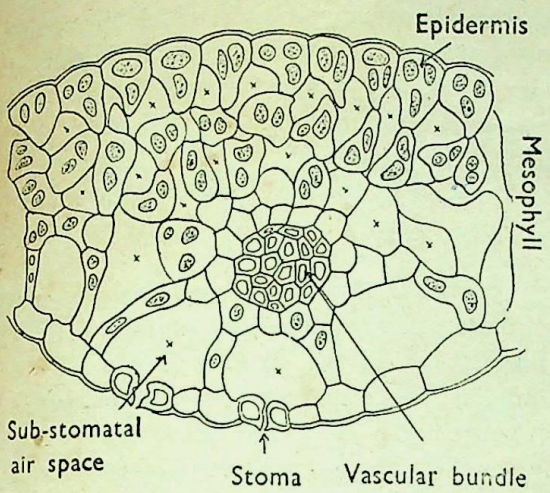

FIG. 27. T. s. of leaf of *Selaginella*. Note the large number of intercellular spaces which have been marked with crosses.

Vegetative Propagation. It is of rare occurrence and may take place by fragmentation, *e. g. S. rupestris* or by **bulbils** or by small **tubers**, *e. g.*, *S. chrysocaulos* and *S. chrysorhizos*.

Reproduction. The reproductive structure is a compact one and develops at the terminal portions of the branches. It is called a **strobilus** or **spike**. Usually it tapers towards the apex and the length varies from 1/4th of an inch to 2-3 inches in different species. Mention must be made of

FIG. 28. Diagrammatic L. s. of strobilus of *Selaginella* of an erect species showing microsporangia above and megasporangia below. *A*, strobilus axis ; *B*, Ligule ; *C*, Megasporangia; *D*, Tetrad of megaspores ; *E*. Microsporangium ; *F*, Tetrad of microspores.

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S. patula and *S. cuspidata* the two abnormal species in which the terminal portion of the branch may continue vegetative growth beyond the spike and in a vegetative shoot. *S. erythropus* furnishes an interesting example where a second strobilus is produced on a fertile branch after an intercalary sterile portion. The strobililus is either erect or horizontal. In some cases the strobili due to the loose arrangement of sporophylls become inconspicuous.

A strobilus possesses many ligulate **sporophylls,** each bearing on its upper side and near its base a small short stalked **sporangium**. But the sporangia, instead of being all alike are of **two** distinct kinds. Both of these two types are present on the same strobilus. One type of sporangia contains four large spores and the other contains very many small spores (Fig. 28). The large spores are the **megaspores** and the sporangium which contains them is the **megasporangium** and the leaf on which it is borned is a **megasporophyll** similarly the small spores are **microspores,** their respective sporangium is the **microsporangium** borne on a **microsporophyll** Each sporophyll like the leaf has got a ligule in its axil. This **dimorphic** condition of spores is known as **heterospory** (Fig. 29).

Distribution of micro and megasporangia. The distribution of micro and megasporangia on the axis of the strobilus depends upon the form of the plant. But in some cases the strobilus contains either micro or megasporophylls alone as in *S. gracilis*. If it is erect, the lower sporophylls are megasporophylls and the upper ones are microsporophylls. If it is prostrate the sporophylls on the ventral side possess megasporangia and those of the dorsal side microsporangia e. g. *S. Oregana* and *S. inaequalifolia*. In most cases the strobilus bears two types of sporophylls as seen in *S kraussiana* and *S. helvetica*. Generally it is seen that the megasporangia are always towards the soil irrespective of the form which the plants may assume.

Development of Sporangia In most cases the sporangia are **cauline** and arise from the cells of the axis, whereas Bower regards them of **foliar** nature due to their development from the base of the sporophyll. (Fig. 30).

The Sporangia are **eusporangiate** in development.

All sporangia whether developed from a single initial cell or a row of initial cells develop alike to the stage at which they contain numerous spore mother cells. In the microsporangia almost all spore mother cells divide meiotically to form a tetrad of four spores each. The result is the production of a large number of haploid **microspores** within a microsporangium.

Megasporangium

Tetrad of megaspores

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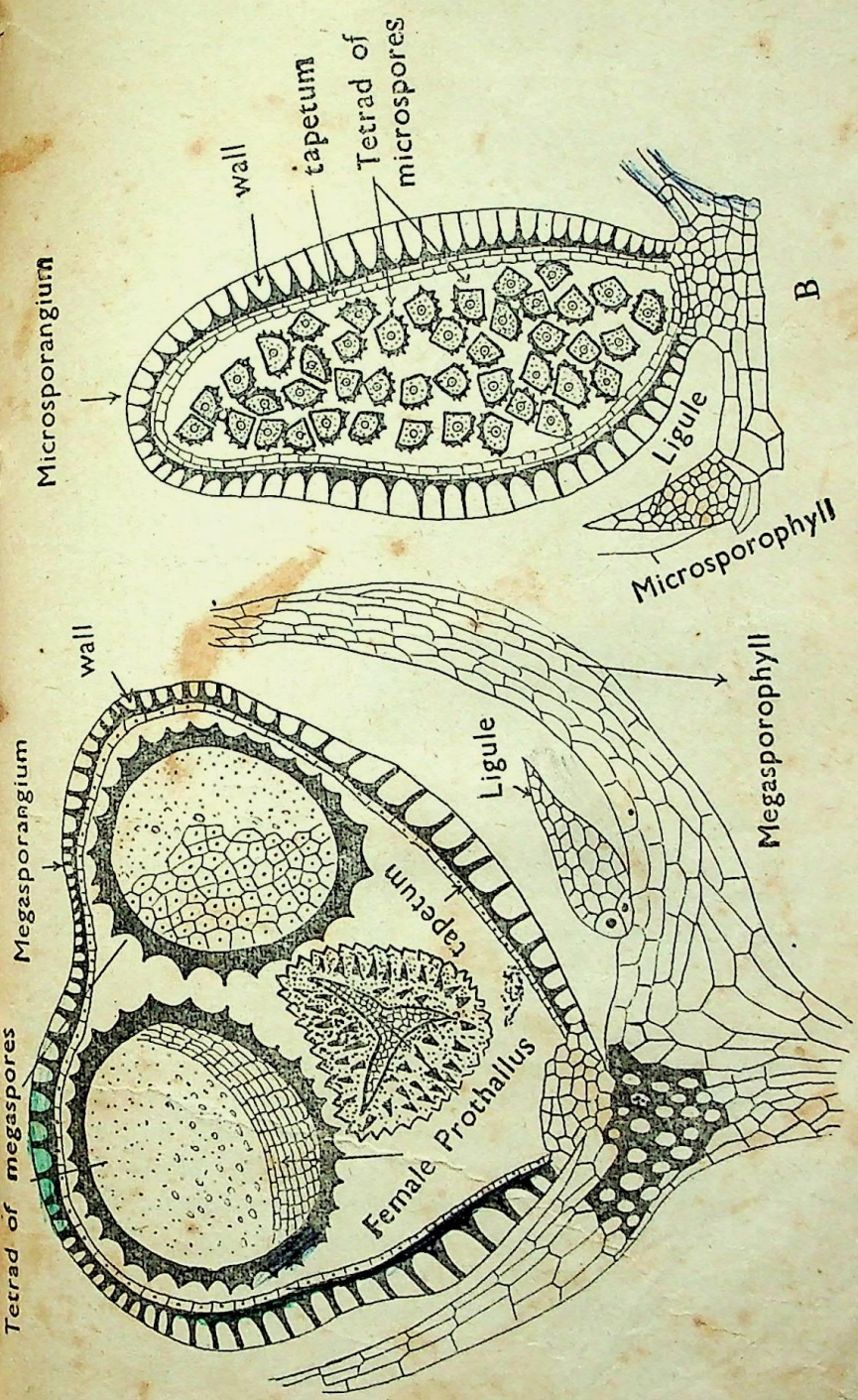

FIG. 29. *A*, L. s. of the megasporangium ; *B*, L. s. of microsporangium

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The case with the megasporangium is entirely different here all the spore mother cells except one usually disentegrate. The remaining functional mother cell divides meiotically to form four **megaspores**. These increase in size and develop thick corrugated wall.

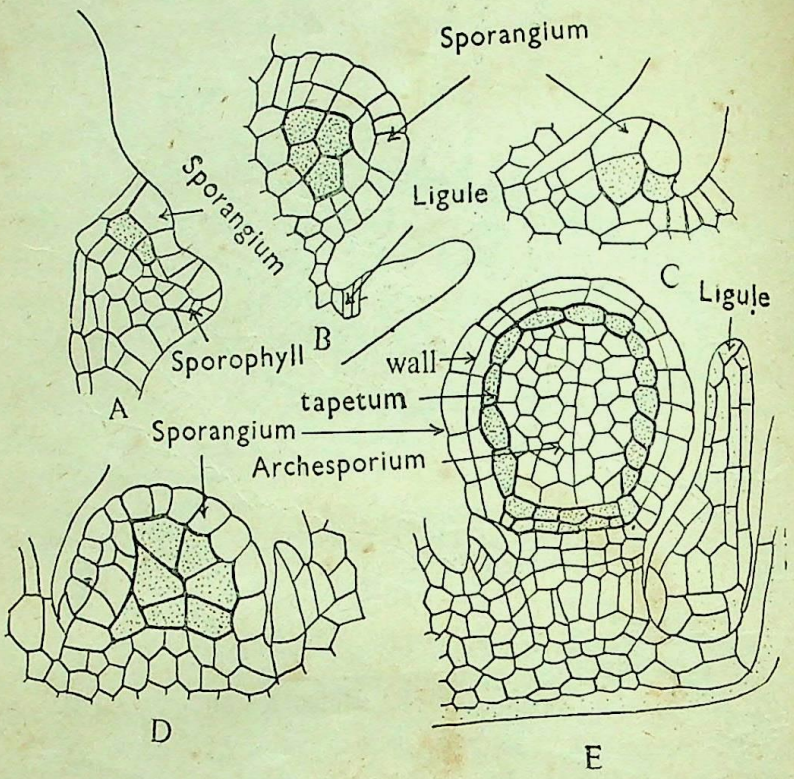

FIG. 30 Development of sporangia of *Selaginella*. A-*B*, showing cauline origin of sporangia ; *C-E*, stages showing foliar development of sporangia.

Sometimes more than one megaspore mother cell functions and the result is the accumulation of more than four megaspores *e. g.*, *S. willdenovii* with 24 spores. The number may be as few as one as in *S. rupestris*. The **sporangial initial** or initials divide periclinally into an outer **jacket initial** or initials and an inner **archesporial initial** or initials which by further repeated divisions form the **sporogenous tissue**. The former follows the latter and produces a two celled thick **wall**. Within this lies the **tapetum** a nourishing sterile sporogenous tissue. Duerdon (1929) regards this an **atavism** which points to the homologous nature of the micro and megasporangia. The mature microsporangium is red, yellow, or brown on account of the contained microspores. The megasporangia are paler greenish and contain chalky white, yellow or orange megaspores. The megasporangium is four lobed organ as compared to a regular smooth microsporangium. Thus the megasporangium is larger

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contains four larger cream coloured megaspores while microsporangium is small and contains numerous small spores.

Germination of Spores. The difference in size between the two kinds of spores is associated with a difference in their function. The megaspore develops into a female gametophyte while the microspore into a male gametophyte. The microspore except for its much smaller size

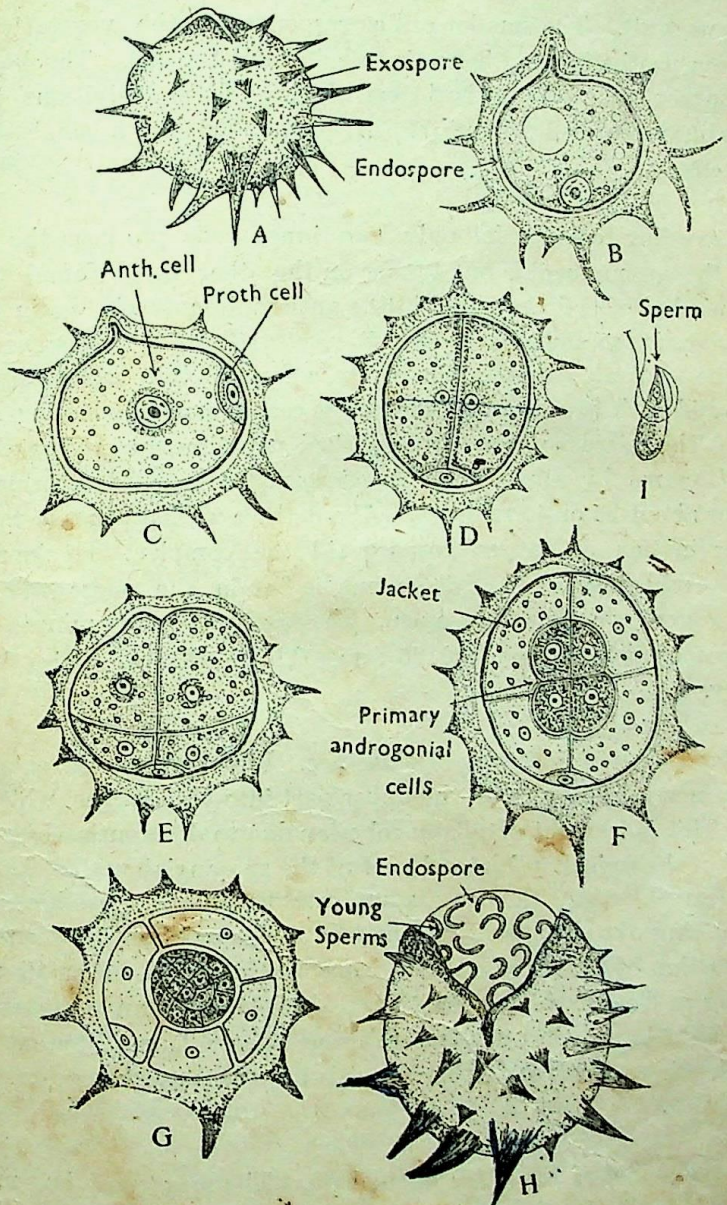

FIG. 31. *A—H.* Stages in the development of male gametophyte of *S. kraussiana.*

and red colour closely resembles a megaspore. It germinates into a 13

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celled male gametophyte while still in the microsporangium thus differing from other pteridophytes. The spores of *Selaginella* are peculiar in that they show intrasporangial germination called "**precocious**" by Bold (1957). So that at the time of liberation the spores are found to be in various stages of gametophyte development.

Germination of Microspore. The first division results in the formation of a large and a small cell both of which lie within the microspore wall. The smaller cell corresponds to the vegetative tissue of the fern prothallus and hence is called **prothallial cell**. The larger cell is the mother cell of the antheridium which by further divisions develops a central group of 6–8 primordial cells surrounded by a single layer of **jacket cells**. (Fig. 31)

According to Millardet only two inner cells produce the mother cells of the spermatozoids but Pfeffer on the other hand found that all the primordial cells first formed in the antheridium divide again and at length give rise to **antherozoids** *e.g. S. martensii* and *S. caulescens*. Each cell of the central group is finally transformed into a spirally coiled antherozoid with two flagella, the jacket cells meanwhile having disentigrated. The microspores are usually shed sometime during the development of sperms by rupturing the microsporangia. The spermatozoids move for about 30 or 45 minutes. About three weeks time is taken for the germination of the microspore till the complete development of sperms. When mature the 256 sperms lie free in the spore wall which liberates them when it bursts open. The sperms are very minute in size roughly measuring about 0·0125 mm. Their cilia are twice long as the body.

Mechanism of Sporangial Dehiscence. When mature the sporangium splits open vertically only in the upper part into two valves which gape apart. This is brought about by cohesion due to differential hygroscopic changes in the apical and lateral part of the sporangial wall. The basal portion (unsplitted) of the sporangium dries up and becomes boat shaped finally forcing out the spores violently at a distance of few centimeter. The liberation of the spores takes place at intervals in small masses. According to Goebel this violent dispersal of spores is an adaptation for cross fertilization in that it helps to bring spores from different plants near each other. This is further proved by the **protandrous** nature of the strobilus.

Development of Female Gametophyte. The megaspore has more or less the shape of a low broad triangular pyramid with a rounded base. Externally their shape is similar to that of microspores except that they are twenty times larger than the microspores. They can be seen easily

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with naked eye. Their size ranges from $1\frac{1}{2}$ mm. to 5 mm. each megaspore has got a characteristic well marked **triadiate ridge** prolonged into a beak like portion. It is in this region that the spore ruptures. Each has got a very thick rough cutnized sculpture outer wall the **exospore**, and a delicate **endospore** (Fig. 32).

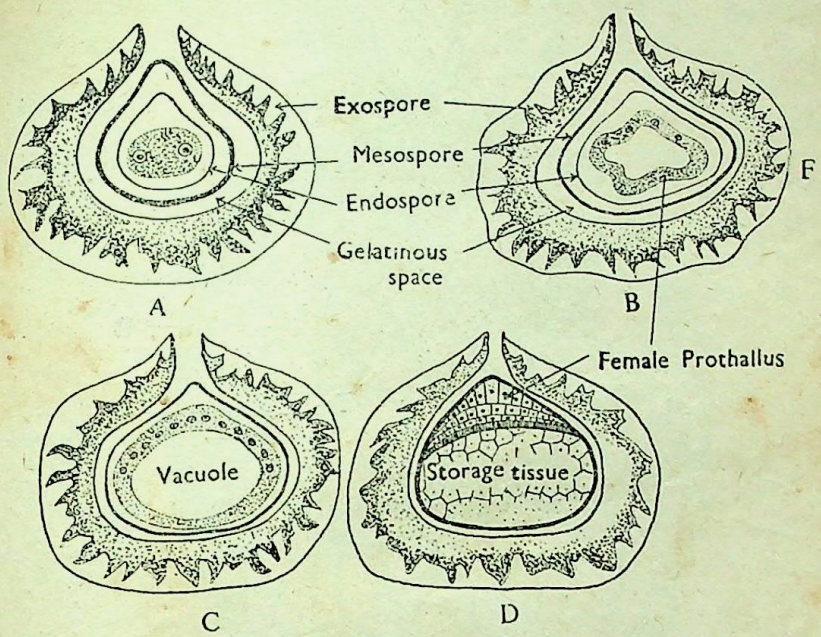

FIG. 32. Development of female gametophyte of *S. kraussiana* *A—B*. Early stages showing contracted protoplast. The exospore and mesospore are separated by a space containing gelatinous membrane ; *C*, Protoplast expanded due to the appearance of a central vacuole. Nuclei divide by free unclear division ; *D*, Protoplast begins to thicken and fills the central vacuole, Cell formation towards the apical and takes place developing a female prothalues which is cut off from the rest of the spore by a diaghragm. Cell formation proceeds in the basal region which forms the storage tissue.

Mostly the megaspores germinate **in situ** *i. e.*, while still enclosed in the megasporangium long before it reaches its full size. The stage at which megaspores (developing female gametophyte) is shed varies from species to species. In some case it is liberated immediately after first division, in others like *S. kraussiana* it may be shed shortly after the development of first archegonia or in some interesting cases the megaspores are not at all liberated from the megasporangium till fertilization has taken place and a well developed embryo is the result *e. g.*, *S. apoda* and *S. rupestris*. (Fig. 33) Campbell (1902) has worked out the development of the female gametophyte in *S. kraussiana*. Here the protoplasm contracts first to a small sac like structure which is accompanied by the rapid expansion of the wall so that the two become separated by a wide space.

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This is followed by the bursting of the outer wall into two layers the **exospore** and **mesospore** which are separated with each other by a **gelatinous membrane.** The megaspore, at this stage contains a haploid

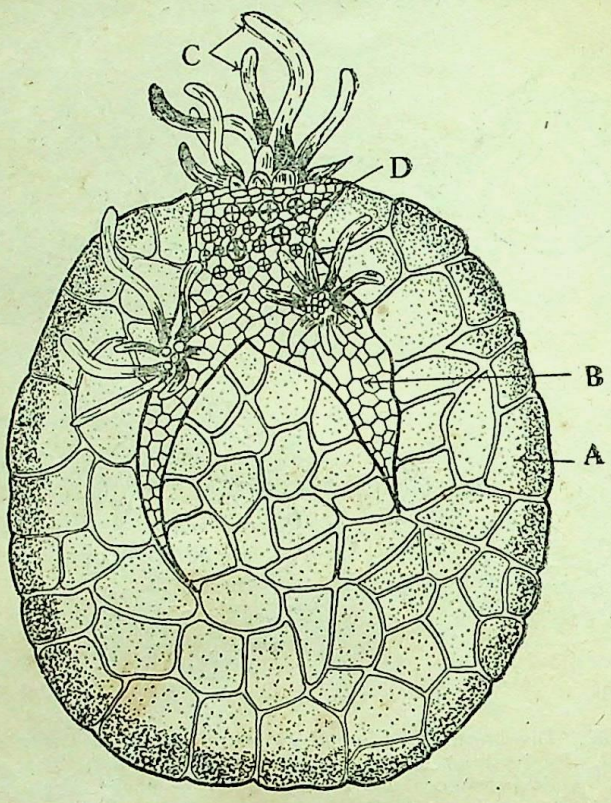

FIG. 33. Ruptured megaspore of *Selaginella* showing exposed prothallial tissue with three rhizoidal humps and archegonia scattered between them ; *A*, Spore wall ; *B*, Prothallial tissue ; *C*, Rhizoids ; *D*, Archegonia.

nucleus which undergoes division producing numerous nuclei around the protoplasmic layer. At this stage the protoplasm increases in size and volume thus establishing contact with the exospore and mesospore and obliterating the central vacuole.

At the beak like portion in the centre of the triradiate ridge, wall formation takes place. This results in the development of a small celled meniscus shaped cellular tissue (Fig. 34) This is one cell thick at the sides and three cells thick in the middle and is called the **female prothallus.** Below this, by free cell formation results a large celled tissue of hexagonal cells called the **diaphragm.** Pfeffer regards them as **secondary**

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prothallium and compares this tissue with the endosperm of Angiosperms.

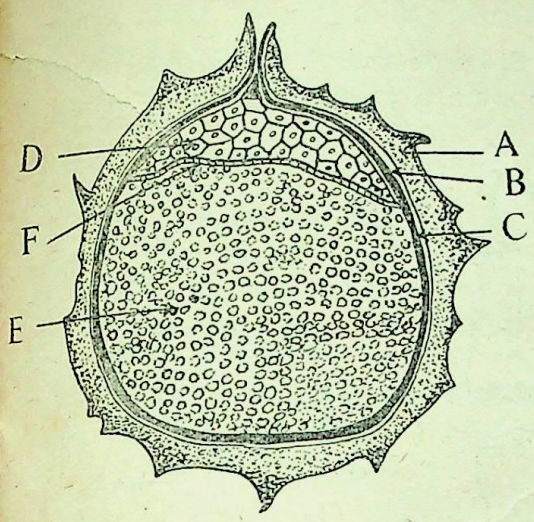

FIG. 34. Vertical section through a developing megagametophyte of *Selaginella* showing female prothallus and storage tissue separated by a diaphragm ; *A*, spore wall ; *B*, Reduced space between exospore and mesospore ; *C*, Mesospore : *D*, Female prothallus ; *E*, Storage tissue. *F*, Diaphragm.

Certain superficial cells towards the apical side enlarge and behave as potential **archegonial initials** and form archegonia. At this stage the megaspore bursts along the ridge exposing the female prothallus. Soon **vestegial rhizoids** develop from three little humps. The archegonial initial divides into two which further divides into four and each of these redivides by oblique transverse divisions into cells that lie one above and other. Thus the **neck** consists of four rows of cells with two cells in each row. The lower cell divides thrusting a narrow prolongation in between the neck cells and this separated off as a **neck-canal cell** and the large cell the **central cell.** This cell further divides and forms a **ventral-canal** cell and an **egg.** When the archegonium is mature the neck canal cells and ventral-canal-cell disorganize forming a mucilagenous product which oozes out from the neck to admit the sperms to the egg (Fig. 35) Generally in *Selaginella* the megasporangia break open thus liberating the female gametophyte which fall to the ground.

Fertilization. Usually the male gametophytes are shed from the microsporangium on the ground where they complete their development ultimately to developspera-matozoids. These are libera ted by the decay of the microspore wall. If the microspores or male gametophyte gets a chance to fall near the mature female gametophyte or megaspore and provided moisture is present, the sperms swim from

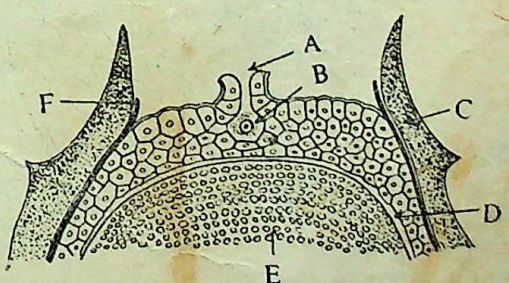

FIG. 35. Vertical section of the megagametophyte of *Selaginella* showing an archegonium ready for fertilization. *A*, Mature archegonium; *B*, egg; *C*, Expose; *D*, Diaphragm ; *E*, Storage tissue.

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the male gametophyte to enter archegonia of the female. The sperm ultimately fuses with the egg resulting in its fertilization.

But in certain cases like *S. apoda* and *S. rupestris* an approach to the **seed habit** is seen. Here when a megasporangium is mature, it

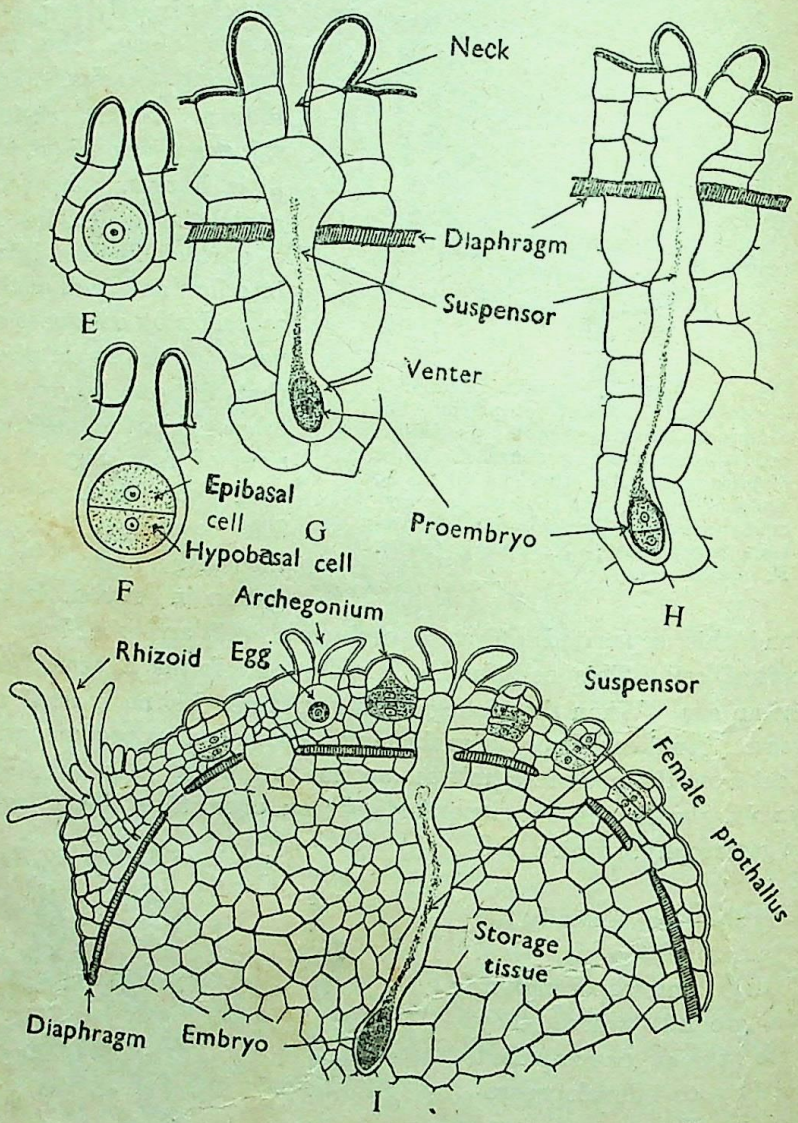

FIG. 36. Development of *S. kraussina* showing the development of suspensor which pushes the embryo deep in the storage tissue ; *E*, zygote ; *F*. Division of zygote into epibasal and hypobasal cell ; *G*, Development of Proembryo and suspensor; *H*,—*I*, Later stages.

cracks open but not sufficiently to permit the escape of developing

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female gametophyte. Only one megaspore is formed in each megasporangium. The microsporangia however, when mature burst open and the developing microgametophytes are thrown out. Some of them shifting down between the sporophytes fall by chance into the partly open megasporangia. Lying now in the megasporangium the two kinds of gametophytes complete their development. If sufficient water is present fertilization takes place. The young embryos develop with in the wall of the megasporangium, and are only dropped when they are already provided with a root and primary shoot. At some time later the opening of the megasporangium becomes larger and the megagametophyte with their developing embryos may fall to the ground.

This is especially significant, since it introduces in the life cycle a close porallel to the **pollination** and **seed formation** habits formed in the

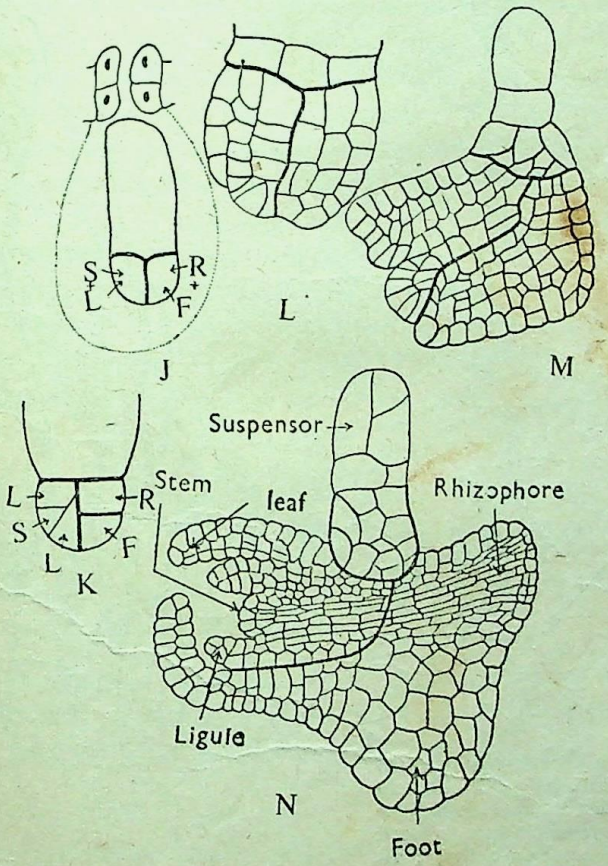

FIG. 37. Later stages (J—N) of embryo development; *S.* stem; *L*, Leaf; *F*, Foot; *R*, Root.

Spermatophytes. Therefore, when the megaspore with its newly formed embryonic sporophyte falls to the groud, it is for all practical purposes a seed and hence the *Selaginella* approaches the seed habit.

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Development of Embryo or Sporophyte. The oosphere gets surrounded by a wall and becomes an **oospore** (Fig. 36). It divides transversely into two cells, the upper **epibasal** and the lower **hypobasal** cell (Fig. 36 F). The former forms the **suspensor** cell which elongates and pierces the hypobasal cell which develops the **embryo** into the tissue of the female gametophyte. According to the Pfeffer such type of development is seen in Gymosperms. The embryo differentiates into **foot**, **root**, primary **stem** with two rudimentary **leaves and rhizophore**

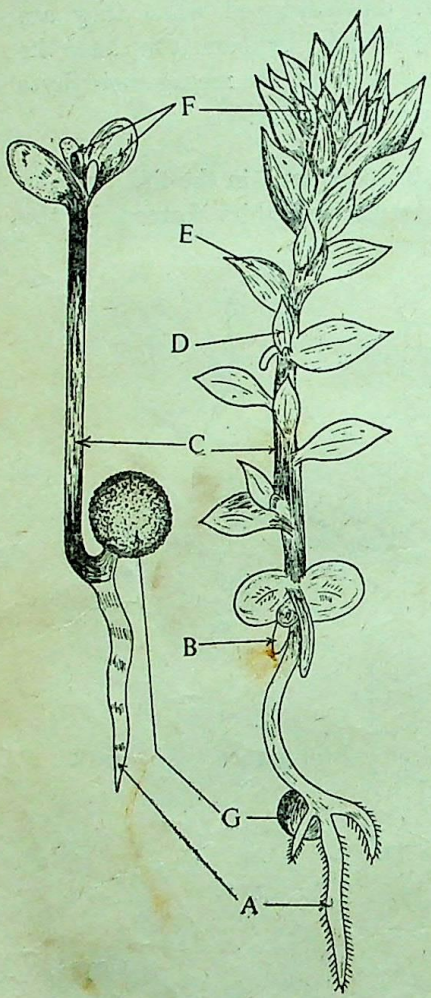

FIG. 38. Older Sporophytes of *Selaginella apoda* still attached to the megagametophyte suggesting resemblance to seed habit of spermatophyte; *A*, Root; *B*, Rhizophore; *C*, Stem; *D*, Small leaf; *E*, Larger; leaf; *F*, Cluster of leaves at the apex on the left is young sporophyte while on the right is older sporophyte.

FIG. 39. Sporelings of *S. apoda* from megaspores which are still *in situ* on the strobilus.

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(Fig. 37). By the outward growth of the stem and root the young sporophyte eventually becomes independent of the gametophytic tissues within the old megaspore wall.

Features of Special Interest in Selaginella.

1. *Selaginella* exhibits an important evolutionary advance over the Pteridophytes, in its development of **heterospory**, which foreshadows the reproductive characterstics found in Spermatophytes. Heterospory is associated with differentiation of sporophytes and sporangia into two types, one of which develops into male, the other into female gametophyte. Thus the difference between the two sporangia is actually a sexual one, even though the reproductive structures are primarily asexual.

2. Associated with this, is the reduction in the size of the gametophytes, their strict heterothallic nature, their dependence upon sporophytic tissues for nourishment, and the transfer of the male gametophyte to the female while each is contained in the old sporophyte structure. These conditions are all duplicated in Angiosperms, hence *Selaginella* approaches closely the formation of seed (Fig. 39).

3. **Precocious** germination of spores in their respective sporangia and their violent dispersal is an adaptation to cross fertilization in that it helps to bring spores from different plants near other. The protandrous nature of the strobilus further supports this.

4. Permanent retention of the female gametophyte in the megasporangium and its fertilization *in situ*.

5. Endogenous formation of the female prothallium shows resemblance to the prothallium in the embryo-Sac of Gymnosperms and even in Angiosperms.

6. Development of suspensor.

7. Elongation of suspensor with compression and absorption of adjacent cells thus thrusting the embryonal cells downwards first into the primary and then in the secondary prothallium, is a Gymosperm character.

8. Completion of the development of the male and female gametophytes in the megasporangium (Fig. 39).

9. Falling off the megaspore, with its newly formed embryonic sporophyte to the ground resembles the seed habit of Spermatophytes (Fig. 38).

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10. Duerdon (1929) reported the presence of **true vessels** in the xylem of a few species like *S. densa, S. rupestris, S. rupicola,* and *S. oregana.*

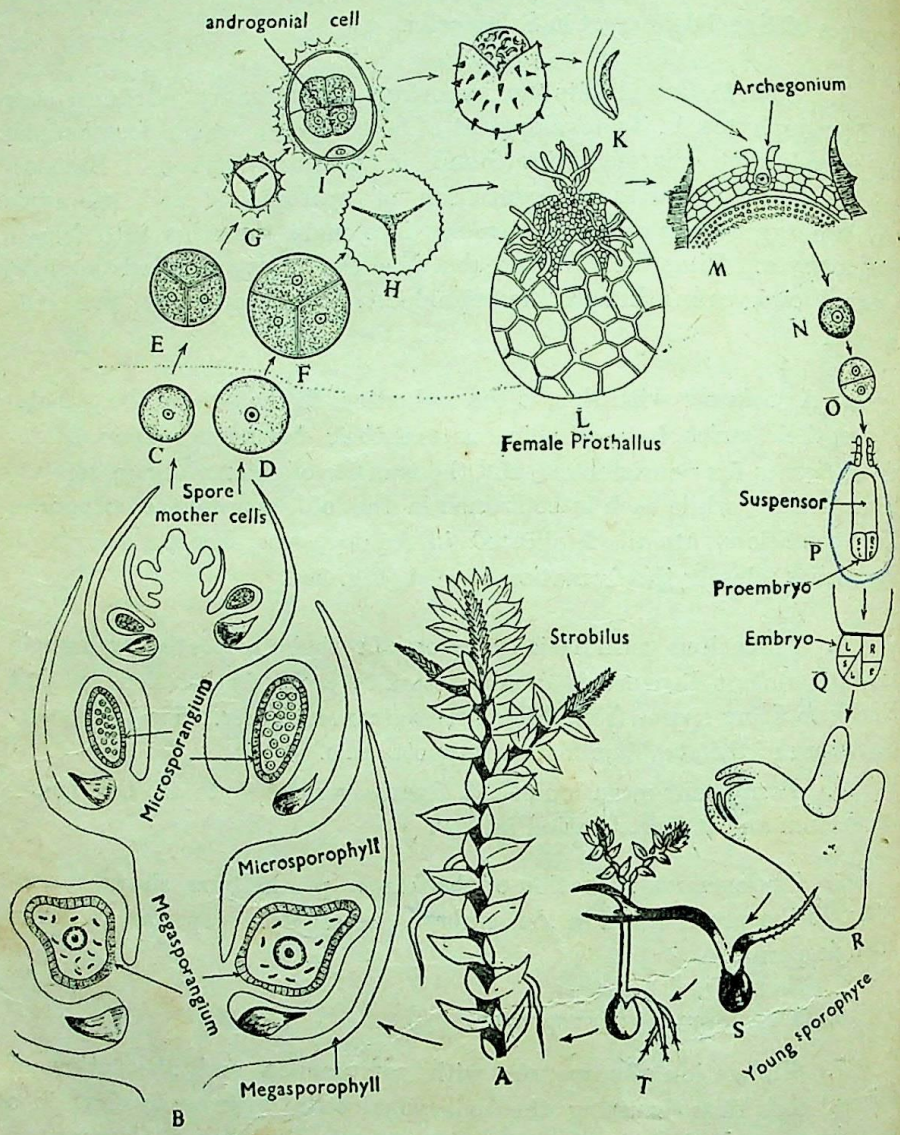

FIG. 40. Diagrammatic representation of the life history of *Selaginella* *A*, Sporophytic plant ; *B*, L. s. of strobilus showing micro—and megaspore mother cells ; *C*, Microspore mother cell (2 x) ; *D*, Megaspore (2 x) ; *E*, Tetrad of microspores (x) ; *F*, Tetrad of megaspores (x) ; *G*, Microspore ; *H*, Megaspore ; *I*, Male gamstophyte ; *J*, Mature male gametophyte with protuding endospore ; *K*, Sperm ; *L*, Female prothallus with archegonia and rhizoids ; *M*, Archegonium awaiting fertilization ; *N*, Zygote (2 x); *O—R*, Development of embryo ; *S—T* Young sporophyte attached to the megaspore.

11. Presence of special organs, the rhizophores.

Economic Importance. Species of *Selaginella*, on account of their feathery moss-like foliage are ornamental objects for table decoration.

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S. caesia and *S. willdenovii* deserve mention on account of their unusual bronze and bluish colours. *S. serpens* is the most interesting species which is remarkable for the periodic changes in the colour of its foliage. In the morning it shows a distinct bright green colour, which changes to pale green during day and at night the original green colour reappears.

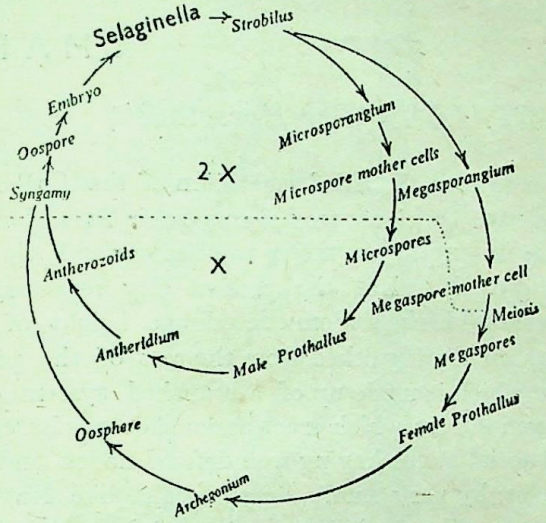

FIG. 41. Life cycle of Selaginella

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CHAPTER 8

EQUISETALES ("*The Horsetails*")

This order formed the chief vegetation of the Corboniferous period and was represented by giant tree forms such as Calamites measuring about 30 meters in length, one meter in diameter and showing well marked secondary growth. But the present day representatives are all quite small perennial herbs seldom exceeding a height of few feet only. The Equisetales are distinguished from the rest of the pteridophytes by the sporophyte which is made up of a branched system of underground horizontal rhizomes from which erect aerial shoots arise each season; by hollow jointed aerial stems having well defined nodes and longitudinally ribbed internodes; by very small simple scale like leaves arranged in whorls to form cone-like strobili at the tips of the aerial shoots ; and by the heavy impregnation of outer tissue with silica.

This order is represented by three families, two of which are represented as fossils and the Equisetaceae is the only family which is represented by the living genus *Equisetum*. Rothmaler (1944) has split the genus into two subgenera : *Equisetum* and *Hippochaete* but we do not see any serious reason for splitting it. We shall describe the life history of *Equisetun* as a representative of this group.

EQUISETUM

Systematic position :

Division—*Trachaeophyta*
Sub-division—*Sphenopsida*
Class—*Equisetineae*
Order—*Equisetales*
Family—*Equisetaceae*
Genus—*Equisetum*

Distribution and Occurrence. *Equisetum* comprises about 30 species and is of world wide distribution except Australia and Newzealand. It thrives in a wide variety of habitats. Certain species are familiarly known as **"pipes," "horsetails,"** and **"scouring rushes."** The name

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Equisetum has been derived from a latin word (*equus*=horse+*saeta*=bristle) and hence known as "*horsetail*". Some species grow in shallow ponds and swamps *e. g.*, *E. hyemale, E. sylvaticum* and *Equisetum palustre* ; others in meadows and damp shady places *e.g.*, *E. pratense* ; and still

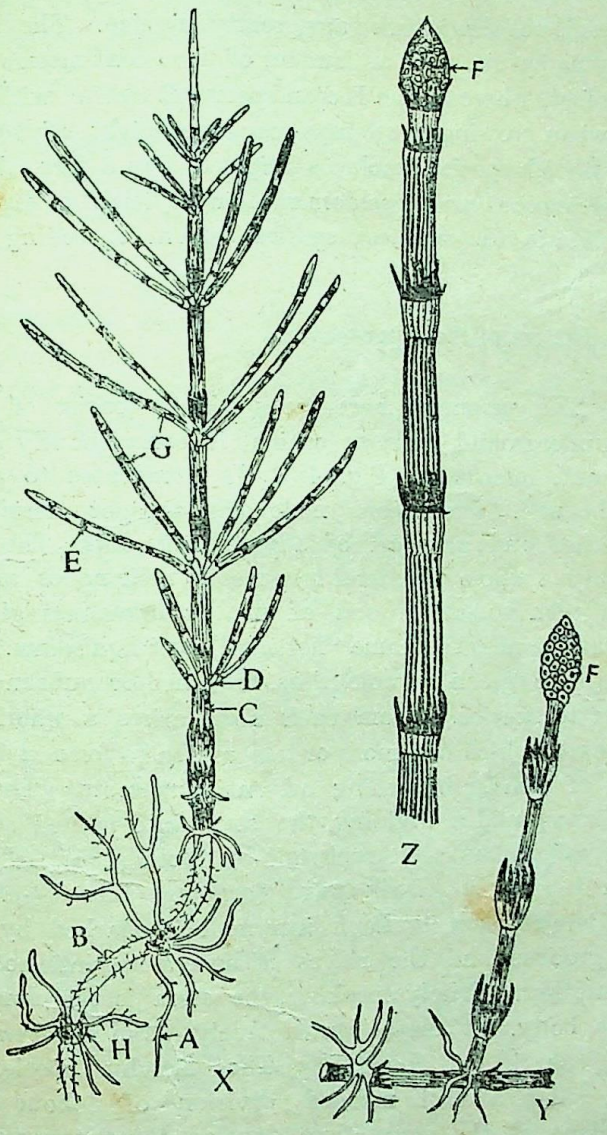

FIG. 42. Habit of *Equistum*. *X*, Portion of vegetative shoot of *Equisetum arvense*; *Y*. Reproductive shoot ; *Z*. E. *hyemale* vegetative shoot with terminal strobilus. (*A*, Root; *B*, Rhizome; *C*, Stem; *D*, Branches; *E*, Node; *F*, Strobilus *G*. Internode; *H*, Tuber.)

others in relatively dry and exposed situations such as sandy embankments *e. g.*, *E. arvense*. In India *E. arvense* is very common in the hills

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of the Punjab. *E. debile* is a very common species found by the side of rivers in sandy soil and extends from Himalayas and Ceylon to eastern Pacific Islands. The largest British species reaches a height of 6 to 8 feet.

The species of *Equisetum* vary greatly in size. The tallest South American living species with a diameter of few centimeters grows to a height of 40 feet, where as the Indian species *E. debile* with a diameter of 1/2 cm., when growing in swamps reaches a height of 10 to 15 feet. The largest British species reaches a height of 6 to 8 feet. But most of the other species are smaller seldom reaching a height of few feet only.

E scirpoides is the smallest species seldom exceeding a height of 20 cm

External Characters of the Sporophyte.

Stem. The perennial herbaceous plants consist of a horizontal branching underground **rhizome** which is conspicuously differentiated into **nodes** and **internodes** (Fig. 42). It penetrates to about a yard or so in the soil. From each node arise upright aerial **sterile** and **fertile** branches and a whorl of adventitious roots. The sterile green branches have a whole of **lateral branches** to their nodes and the lateral branches in turn possess whorls of smaller **branchlets** giving a busy appearance and hence the name **"horsetail"** or **"Equisetum."** The fertile branches may be green or colourless, branched or unbranched differing from species to species. From each node arises a **whorl** of slender, scale-like leaves which are more or less united to form a **brown sheath** and a whorl of slender branching adventitious roots. The aerial stems have conspicuous nodes dividing the stem into **jointed sections** hence the group is referred as **"Arthrophyta"** by Bold (1957). The name has been assigned after a Greek word (*arthros*=jointed+*phyton*=plant) meaning **"a jointed plant."** Each internode is marked by longitudinal ridges and grooves and the ridges of successive internodes alternate with one another. Truely speaking, the stem is the dominant organ of the plant body. It may branch freely, as in *E. arvense*, or remain unbranched, as in *E. hyemale*. The marshy species, such as *E. palustre*, show a well marked division of labour in that on the same plant at the same time develop three types of branches: (1) **Sterile** richly branched green branches. (2) **Fertile** non-green short lived branches. (3) **Intermediate** type, which are fertile, non-green, and unbranched in the beginning but after the disorganization of the strobili become green branch and persist.

Leaves. Each node of an aerial branch bears a brownish sheath of small, scale like uninerved **simple leaves** somewhat similar to those on

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the underground stem. Their number ranges from 3 to 40 in one whorl. These remain photosynthetic for a short period after their formation, and soon become dry and scale-like. The leaves are only protective in function. The leaves of successive nodes being arranged in **alternate** fashion. The bases of the leaves are fused and give the appearance of a scalloped collar. The leaves originate as superficial, ring-like outgrowths of the nodal cells.

Roots. The **adventitious** roots arise in whorls at the nodes of the subterranean rhizome. They live for a number of years without adding anything to their length, though they are slender, fibrous, and **endogenous** in nature.

Anatomical Structure.

Stem. The general outline of the transverse section of an internode of an aerial shoot is wavy (Fig. 43) on account of the **ridges** and **grooves**.

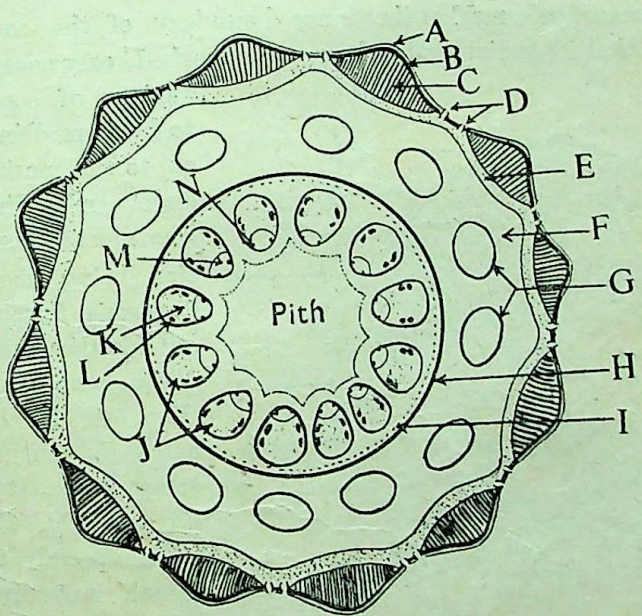

FIG. 43. Diagrammatic T. s. of *Equisetum* Stem *A*, cuticle; *B*, Epidermis; *C*, Sclerenchymatous hypodermis; *D*, Stomata; *E*, Assimilatory tissue; *F*, Cortex; *G*, Vallecular canal; *H*, Endodermis; *I*, Pericycle; *J*, Vascular bundles; *K*, Phloem; *M*, Carinal canal; *N*, Protoxylem; *O*, Pith.

Outside, there is a single layered ill preserved **epidermis**. The thick outer walls of the epidermal cells are impregnated with **silica**, hence the

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stem is hard and rough to touch. On account of silica deposit the ash of the plants was used for polishing purposes and earned for them their old name of "**scouring rushes**". Below each ridge, the cortex contains a vertical strand of sclerenchyma, which contribute to the support and rigidity of the stem. But below each groove, the cortex consists of patches of chlorenchyma, which take the place, physiologically, of the much reduced leaves. Close beneath this assimilatory region lies a large vertical intercellular air cavity called the **vallecular canal**. The **stomata** are confined to each groove and are **sunk** beneath the surface. They are peculiar in that the guard cells are completely covered externally by a pair of **subsidiary cells**, so that a double set of guard cells one above the other appears to be present (Fig. 46-II). The stomata open into intercellular spaces bordered by chlorenchymatous cells. The cortex below the sclerenchymatous **hypodermis** is formed of parenchymatous cells, which alternate with vallecular canals. Thus the inner cortex consists of parenchymatous cells which are interrupted by large vallecular canals, which form an aerating system. (Fig. 44).

The **endodermis** marks the inner boundary of the cortex. It is peculiar in that its radial walls show well marked **casparian bands.** A variety of conditions are to be formed in the genus as to the position of the endodermis (Fig. 45 A,B,C) The most common condition being where the endodermis forms a sheath outside the vascular bundles as seen in *E. palustre* (Fig. 45 A) *E. telmatia* and *E. scirpoides.* In some cases, such as *E. litorale* (Fig. 45 C) there is a special endodermal sheath surrounding each vascular bundle, whereas others like *E. sylvaticum,* (Fig. 45 B) besides the outer endodermis, show an **inner endodermis** delimiting the pith. Below the endodermis, lies a single layered **pericycle**, which forms the external layer of the stele.

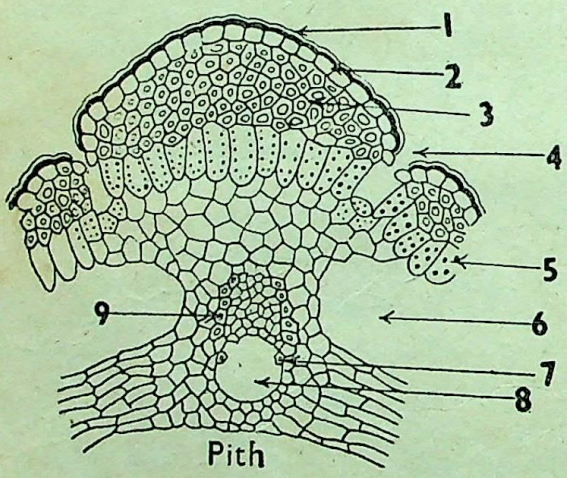

FIG. 44. T. s. of stem of *E. arvense.* 1, Cuticle ; 2, Epidermis ; 3, Sclerenchymatous hypodermis ; 4, Stoma ; 5, Assimilatory tissue ; 6, Vallecular canal ; 7, Protoxylem ; 8, Carinal canal ; 9, Metaxylem.

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The **stele** is of **siphonostelic** type and consists of a ring of vascular bundles hence called the **eustele** or poly-fascicular siphonostele. Accord-

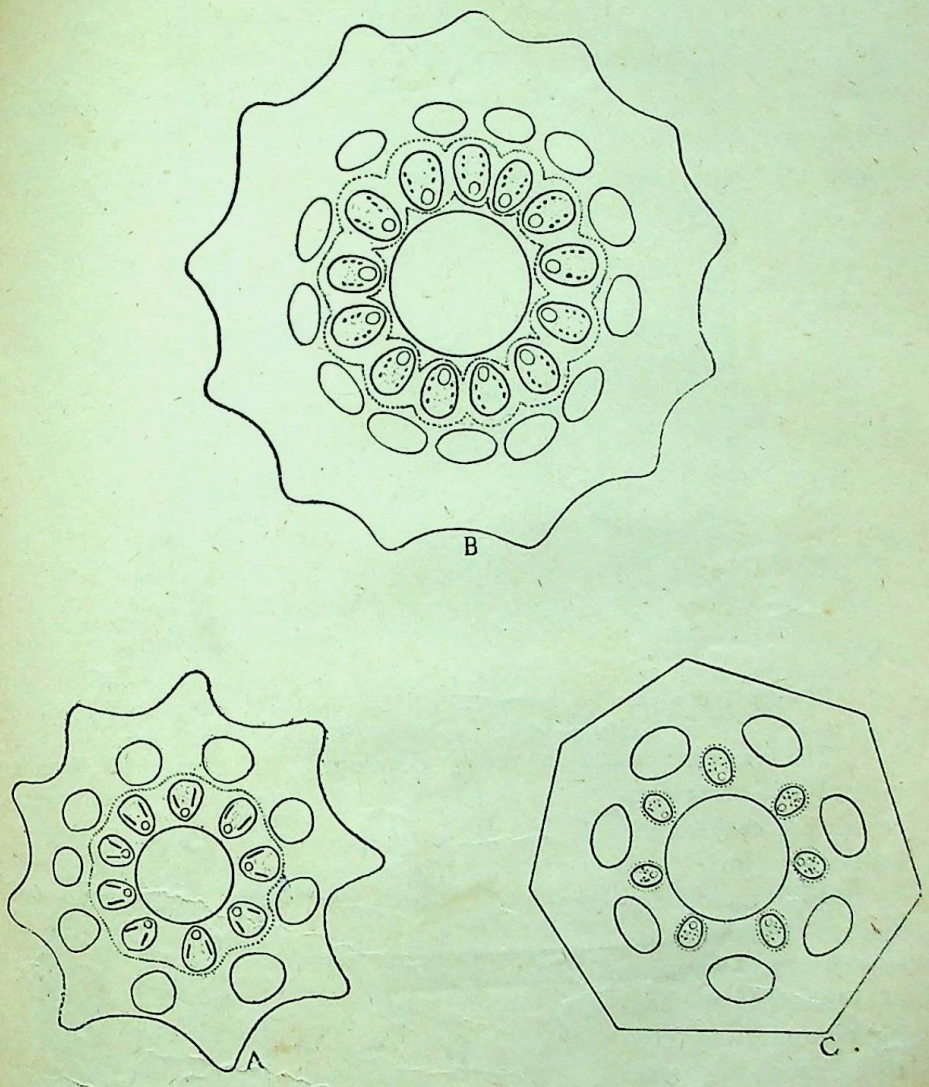

FIG. 45. Range of Endodermis in various species of *Equisetum A*, *E. palustre* stem, (diagrammatic T.s.); *B*, *E. sylvaticum* rhizome, diagrammatic T. s. ; *C*, *E. litorele* rhizome dia grammatic T. s. The endodermis is shown with a dotted line.

ing to Miss Barrat (1920) such a widely perforated siphonostele or eustele has developed from an ancestral form with a solid-protostele, which is seen in the stem of embryonic sporophyte.

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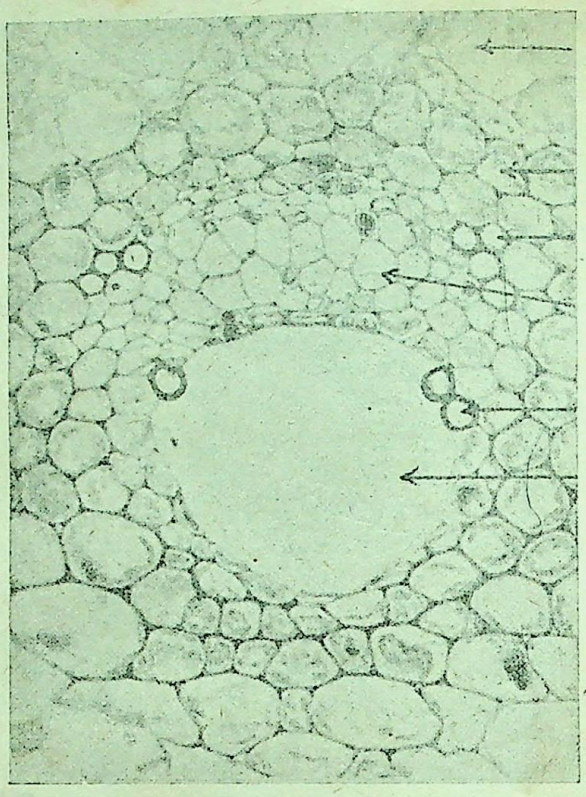

FIG. 46 I. Photomicrograph of a stem of *E. arvense* showing details of a vascular bundle; 1, Vallecular canal ; 2, Endodermis ; 3, Metaxylem ; 4, Phloem ; 5, Protoxylem ; 6, Carinal canal.

The vascular tissue is poorly developed. The **vascular bundles** instead of being concentric are **conjoint** and **collateral** and are separated by parenchymatous **gaps**. Each vascular bundle consists of **'V' shaped xyem** having phloem in between the limbs of xylem (Fig. 46-I). In very young bundles, the endarch protoxylem consists of annular and spiral tracheids but on maturity they separate from one another and thus organise forming a **carinal canal**. This lies opposite the ridge and alternates with the vallecular canal of the cortex.

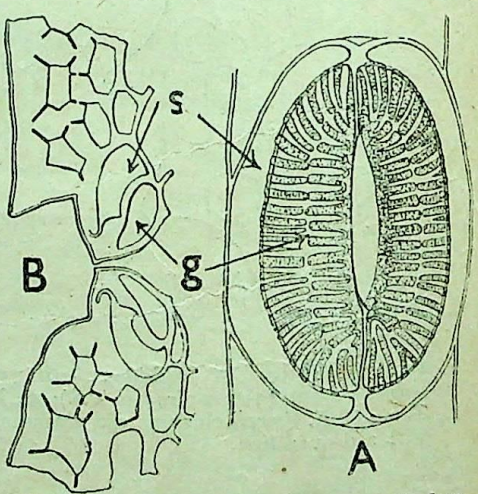

FIG. 46 II. Stomata of *Equisetum* ; *A*, Surface view of the inner surface. The guard cells (g) are covered by a pair of superposed subsidiary cells (s) ; *B* T. s. showing sunken nature. The narrow opening is guarded by his flat guard-cells, which are surrounded by subsidiary cells.

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cell also divides transversely but only once resulting in the formation of an egg and a **ventral canal cell** (Fig. 24, E, F). Now three jacket initials also divide transversely. As the archegonia are embedded in the tissue of the thallus, the position and further development of the jacket initials is not very clear. But one thing is quite certain that cells on the lower side of the egg are not derived from the archegonial initial and therefore they cannot be taken as a part of the archegonium. So a fully mature archegonium is flask shaped with a clear neck and a venter containing a prominent egg. The cover cells are slightly projected outside the thallus (Fig. 24, G).

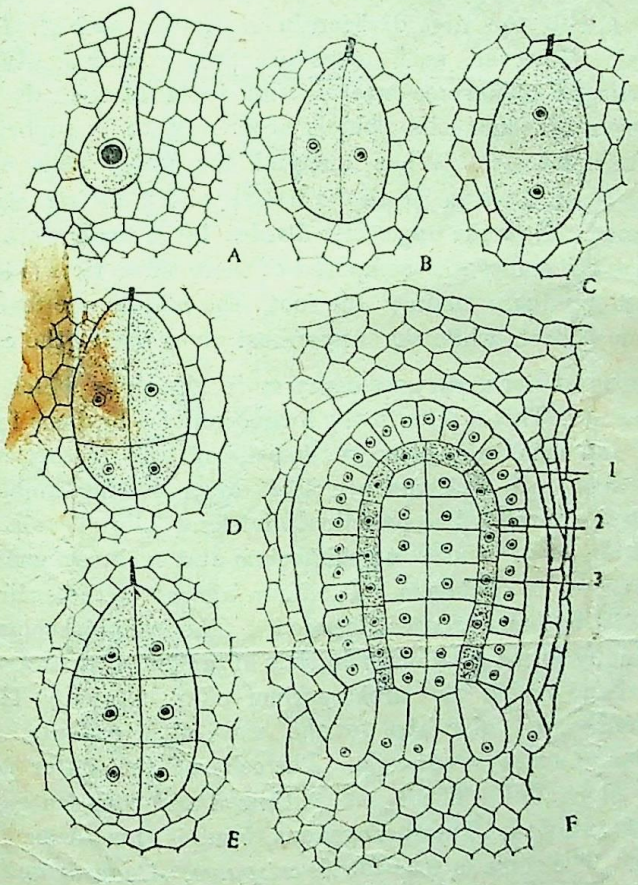

FIG. 52. Fertilization and post fertilization stages in *Anthoceros*. A, archegonium just after fertilization. B, C, different species of *Anthoceros* showing first division in the oospore—longitudinal and transverse. D, E, further divisions in the oospore. F, sporogonium being differentiated into 1. Jacket, 2. archesporium and 3. columella.

Fertilization. At the time of fertilization the neck canal cells along with the cover cells disorganize and are converted into mucilage. Thus a clear passage is formed for the entry of the antherozoids into the archegonium. Many antherozoids are attracted towards it but finally

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only one gets inside. The nucleus of the male unites with that of the female resulting in the formation of an **oospore**. The latter, in the beginning, is small in size, but just after fertilization it occupies the whole of the venter and secretes a wall outside.

Post fertilization stages. The oospore soon enlarges (Fig. 25, A) and undergoes divisions. Usually first division in an oospore is vertical (Fig. 25. B) though according to Pande (1932) there are few species where first division is transverse also (Fig. 25, C). Bharadwaj (1950) has definitely recorded transverse division in case of *A. crispulus*. According to Hofmeister (1862) first division is oblique in *A. laevis*. According to Campbell (1940) the first division in *A. laevis* and *A. fusiformis* is longitudinal. However, such cases are not common. When first division is vertical a transverse wall is laid down afterwards resulting in the formation of four cells, which according to Campbell may be of equal or unequal size. When unequal the upper cells are bigger (Fig. 25, D). Next division is also vertical and thus an eight celled embryo is formed. Now the upper tier divides by a transverse wall and so at this stage the embryo is composed of these three tiers (Fig. 25, E). The lowermost produces mainly the **foot**, the middle one forms partly the foot and mostly **seta** while the uppermost gives rise to the **capsule**.

The lowermost tier undergoes many more divisions which may be regular or irregular. This results in the formation of a bulbous foot. More important developments take place in the cells of the upper tier. Here one or two transverse divisions are laid down so the number of tiers increases to two or three. The periclinal divisions follow soon resulting in the formation of an outer **amphithecium** and an inner **endothecium**. The latter gives rise to columella. It is four layered in the earlier stages but later on it becomes sixteen layered. The amphithecium again divides periclinally forming an outer initials of jacket layer and an inner sporogenous tissue called the **archesporium** (Fig. 25, F). The former divide periclinally and give rise to the wall of the capsule, generally made up of four to six layers of cells. The cells of the outermost layer are vertically elongated. These are cutinized and constitute epidermis which possesses stomata. The sporogenous tissue is thus formed from the amphithecium. The same is true for *A. crispulus, A. laevis and A. fusiformis*.

The sporogenous tissue or archesporium arches over the columella. It may be one to four cells thick. Finally the sporogenous tissue gets differentiated into spores and elaters. The haploid spores are formed as a result of tetrahedral division of diploid spore mother cells which undergo the usual reduction division. The walls of the elaters may be smooth, thick or possess spiral thickening. In the case of *Anthoceros*, they have been termed pseudoelatres, though in function they are similar to the true elaters.

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The metaxylem lies on the flanks of the phloem forming the two limbs of 'v' shaped xylem. It is formed of small masses if scalariform tracheids which are separated from the cells of the protoxylem by several cells of xylem parenchyma. The phloem lies external to the carinal canal and consists of sieve tubes, and phloem parenchyma. The **pith** in young stems is of parenchymatous nature but mature stems show a central hollow cavity.

In *Equisetum*, unlike Spermatophytes, the protoxylem passes into the leaves, whereas the metaxylem is entirely cauline *i e.*, belongs to the stem alone and has no connection with the leaves. (Fig. 47).

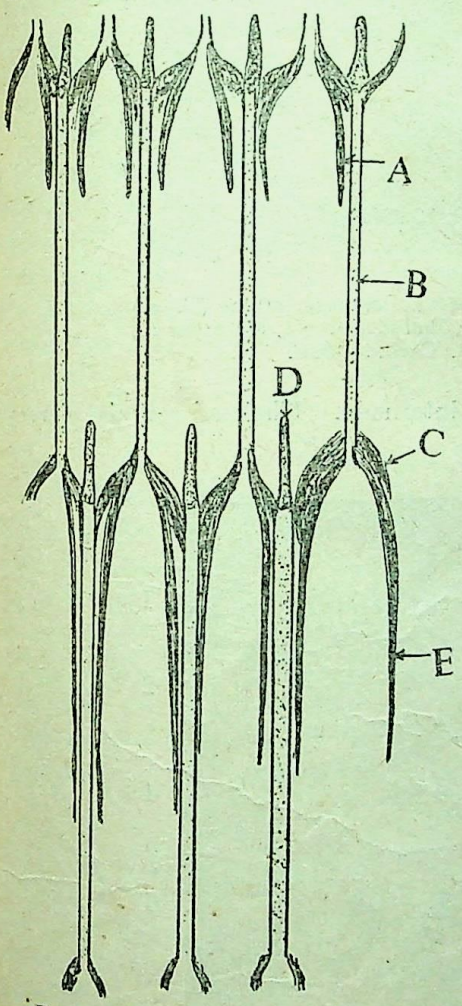

FIG. 47. Scheme of vascular system of *Equisetum*, after Miss Barrat, including the readjustments at two nodes. It suggests the relatively late development of the metaxylem, which gradually extends down the internodes; their length is much reduced.

The lateral branches reveal the same qualitative structure as shown by the main axis, though quantitatively it is different. The number of leaves at each node is reduced to three or four. This leads to corresponding reduction in the number of vascular buudles in the stele and forms the same number of ridges along the internodes.

Thus the stem is **poly-fascicular siphonostelic** and is remarkable for the mingling of **hydrophytic** and **xerophytic** characters. Reduction of vascular tissues, epecially of xylem and the presence of intercellular chambers, are characteristics of hydrophytes. Reduced leaves, and photosynthetic stems with sunken stomata, are characteristic of xerophytes.

Rhizome. The anatomy of rhizome is similar to that of the aerial stem but differs from it, in showing a **simple cortex** without assimilatory cells and stomata, and with **poor development of mechanical tissue** and a **solid pith.** The ridges and grooves are not so well marked as in aerial stem. (Fig. 48.)

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Leaf. The leaves do not serve as organs of photosynthesis but protect the lateral buds. Their lower parts are laterally fused to develop

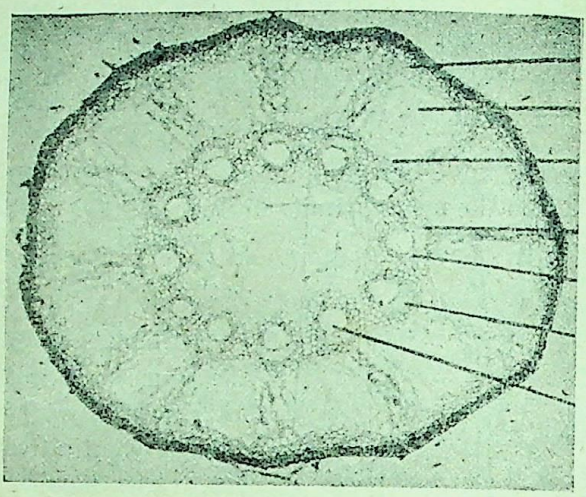

FIG. 48. Photomicrograph of *E. arvense* stem (T. s.) 1, stem ; 2, Vallecular canal ; 3, Endodermis ; 4, Metaxylem ; 5, Protoxylem ; 6, Phloem ; 7, Carind Canal.

a leaf sheath around the base of the internode. The leaf reveals a very

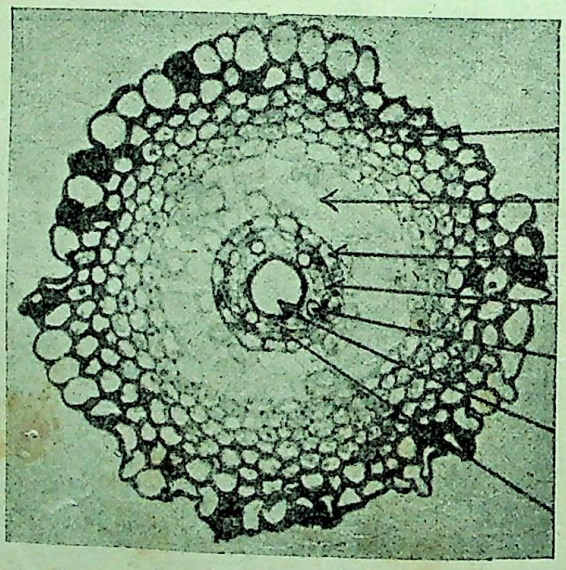

FIG. 49. Photomicrograph of *E. arvense* root (T. s.) 1, outer cortex with exodermis ; 2, Inner cortex ; 3, Endodermis ; 4, Inner endodermis ; 5, Protoxylem ; 6, Metaxylem ; 7, Phloem.

simple structure. There is only one simple collateral vascular bundle,

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which is surrounded by an endodermis. The xylem is poorly developed. Carinal canals are conspicuous by their absence in the xylem. The outer tissues of the leaf sheath consists of narrow bands of sclerenchyma, which pass up the leaf ridges, alternating with the strips of assimilatory tissue associated with stomata.

Root. The adventitious roots display a very simple structure. (Fig. 49.) It has got an outer unicellular **pileferous layer from** which root hairs are given off. Below this, lies a thick multilayered **cortex** which in small roots is divisible into two zones. The outer zone consists of three to four celled **exodermis** formed of highly lignified cells The inner zone is parenchymatous in nature and contains a large number of intercellular air spaces. The **endodermis** is peculiar in that it is **two layered** and is characteristic of the root. It consists of an outer layer of larger cells and an inner layer of small cells. **Pericycle** is absent. Lateral roots arise from the inner layer of the endodermis. **Casparian bands** are only seen in the outer endodermis. The **protostele tri**—or **tetrarch.** In the centre is a large tracheid representing metaxylem with three or four protoxylem groups towards the perephery. In between the angles of the protoxylem lies the phloem. The root grows as a result of the activity of a single three sided apical cell, which produces a root-cap as well as the root tissues.

Vegetative Propagation. Usually it takes place by means of hard brownish hibernating **tubers** (Fig. 42H). They may be pear-shaped or ovoid in shape *e. g.*, in *E. telmateia* and *E arvense.* The internodes swell, become thick, and get separated from parent rhizome behaving as tubers. These possess a store of food and on being separated from the parent plant, are capable of developing new plants. Some species under favourable conditions form at their nodes rudiments of buds and roots which develop new plants as seen in *E. limosum* and *E. schaffneri* and *E. arvense.*

Reproduction. The plant is sporophyte and reproduces by means of **spores.** The spores are found in **sporangia**, which develop on the underside of the peltate, hexagonal **sporangiophores**, arranged in compact cones or **strobili**, at the tip of branches. (Fig. 50). These fertile branches appear in the spring and are some what yellowigh in colour. They differ from species to species. The strobili may develop at the tip of ordinary vegetative branches as in *E. debile, E. myriochaetium*, and *E. hyemale*, or may develop on unbranched, nongreen special fertile branches, which develop from the rhizome as a unit and die after the dissemination of spores *e. g.*, in *E. arvense* and *E. telmateia, E. sylvaticum* and *E. pratense* are intermediate between these two extremes, in that the unbranched

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axis which bears the strobilus lacks chlorophyll at first. It becomes green and branched after the spores have been discharged.

Each cone or strobilus is a terminal structure consisting of a thick somewhat conical **axis** from which are given off at right angles a whorl

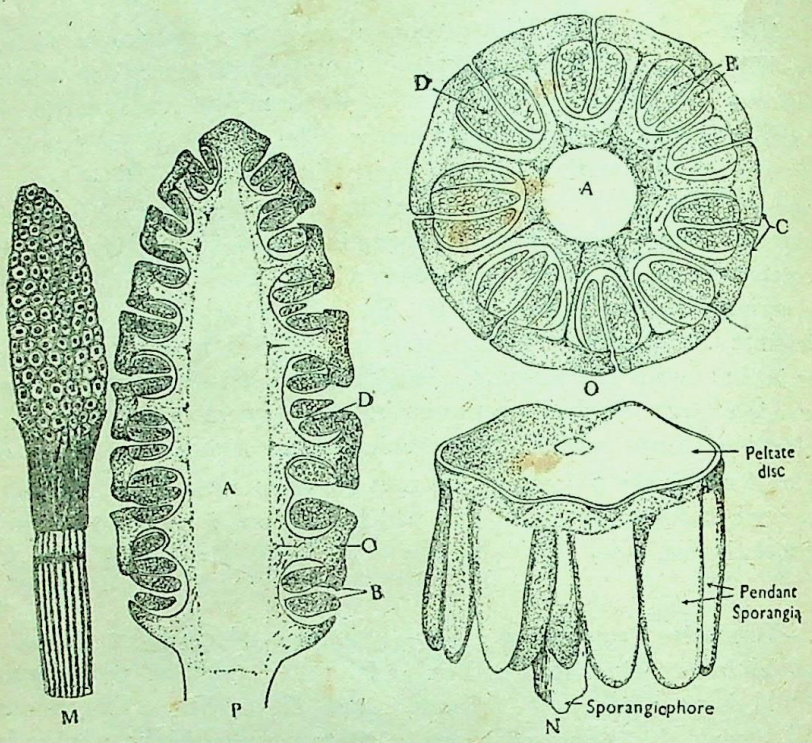

FIG. 50. *Equisetum arvense*. *M*, cone; *N*, A single sporangiophore; *O*, T. s. of cone; *P*, L. s of cone. (*A*, Axis; *B*, Pendant sporangia; *C*, Peltate disc; *D*, Spores

of about twenty densely arranged peltate **sporangiophores** (Fig. 50, O,P). The mature sporangiophores typically are hexagonal in surface view, because of mutual pressure (Fig, 50 N). These fit closely together and form a protective covering for the sporangia which are on the underside of this plate. The lower most whorl is sterile and forms the rudimentary sheath in the form of a collar. There is a ring—like toothed outgrowth **annulus** at the base of the cone.

Milde (1865), Bower (1904), Goeble (1918), Allen (1928), Kashyap (1930), Tochudy (1939) and Sinha (1954) described **some abnormalities** in the cones of Equisetum. Sinha (1954) collected some abnormal cones of *E. debile* from Meerut. One of the specimens was found to have the cone divided into two segments by a narrow transverse constriction having a fertile sheath comparable to the annulus, another specimen showed a short proliferated shoot above the cone.

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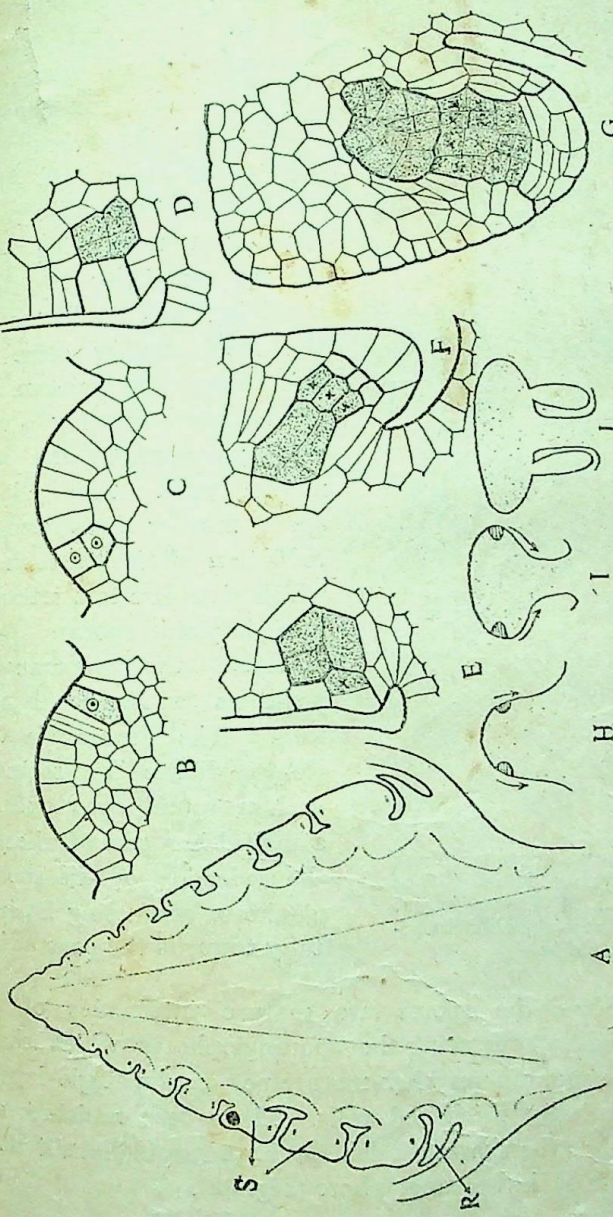

FIG. 51. Development of sporangium of *E. arvense*. *A*, L. s. of a half developed sporangium; *B*, Section of a young sporangiophore showing a sporangial initial; *C*, Division of sporangial initial into an outer cell which forms wall and an inner cell which forms archesporium (shaded); *D*—*G*, Later stages. The cells marked with X have been derived from the outer cell; *H*—*J*, Stages in the development of sporangiophore and inversion of orientation of growing sporangium. (R, annulus; S, Sporangia of *Equisetum*.)

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Development of Sporangium. The sporangium show **eusporangiate** type of development. Each sporangium arises from a single superficial cell on the lower side of the peltate sporangiophore. The **sporangial initial** divides pereclinally into **outer cell** which forms the sporangial **wall** and an **inner cell** which forms the **archesporium** or the sporogenous tissue (Fig. 51). The sporangial wall varies from two to several cells in thickness. The inner most layer of the sporangial wall to next the sporogenous tissue (archesporium) becomes glandular and forms **tapetum.** The cells of the archesporium separate and round off. About one third of them disorganize forming a nourishing liquid for the remaining two third surviving cells. These are the **spore mother cells.** By this time, the tapetum also breaks down forming a nourishing medium for the spore mother cells. The diploid spore mother cells undergo reduction division, each of which gives rise to a tetrad of four haploid **spores.** When mature, the sporangium possesses a single layered wall. The sporangia are elongated sac-like structure with a round apex and are attached in a sort of whorl on the underside of the sporangiophore, projecting horizontally towards the cone axis.

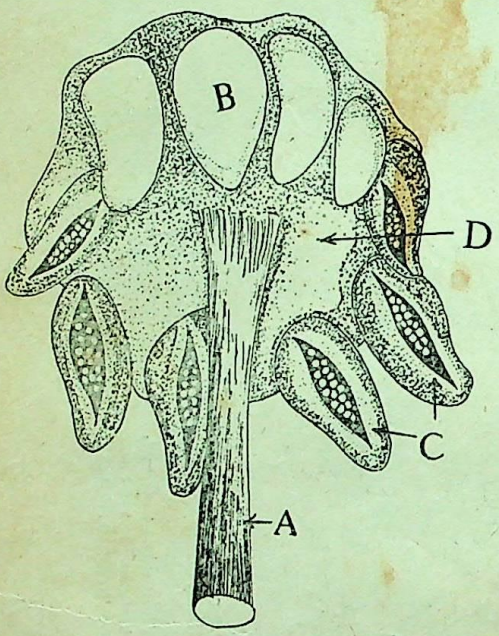

FIG. 52. Ventral view of sporangiophore of *quisetum* are showing dehiscence of sporangia ; *A*, Stalk ; *B*, Sporangia not deshisced ; *C*, Sporangia showing longitudinal slit ; *D*, Peltate disc.

Dehiscence. When the spores are mature internodes of the strobilus elongate slightly separating the sporangiophores which shrink and pull apart. The sporangium when mature possesses a single layered wall composed of spirally thickened cells. These lose moisture and shrink on drying so that the sporangia dehisces by a **longitudial slit** down the side next the stalk of the sporangiophore (Fig. 52).

Spores. The green spherical spores are all alike and are said to be **homosporous.** The young spore when first formed has a thin cellulose wall, but as development continues it becomes more complicated. According to Beer (1909) the wall consists of **four** layers. Each spore besides an inner most yellowish **intine** and a light blue **exine** has got a third

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delicate cuticular layer the **middle layer** which is enclosed by the outer most colourless layer, the **perispore** (Fig. 53). This is thick and splits along spiral lines into long bands which remain attached to the wall of the spore at their middle points so as to appear as four distinct appendages with flat spoon like tips. These peculiar structures are called **elaters** and remain completely wrapped round the spore till the spore is mature and the sporangium dehisces. They are **hygroscopic** and unwind or stretch themselves out as the spores are dried. The elaters twist and uncoil by slight changes in humidity. In moist air they curl up, but when they are dry they stretch out again. The spores are light and are carried away easily by air currents. Each spore is large and contains a

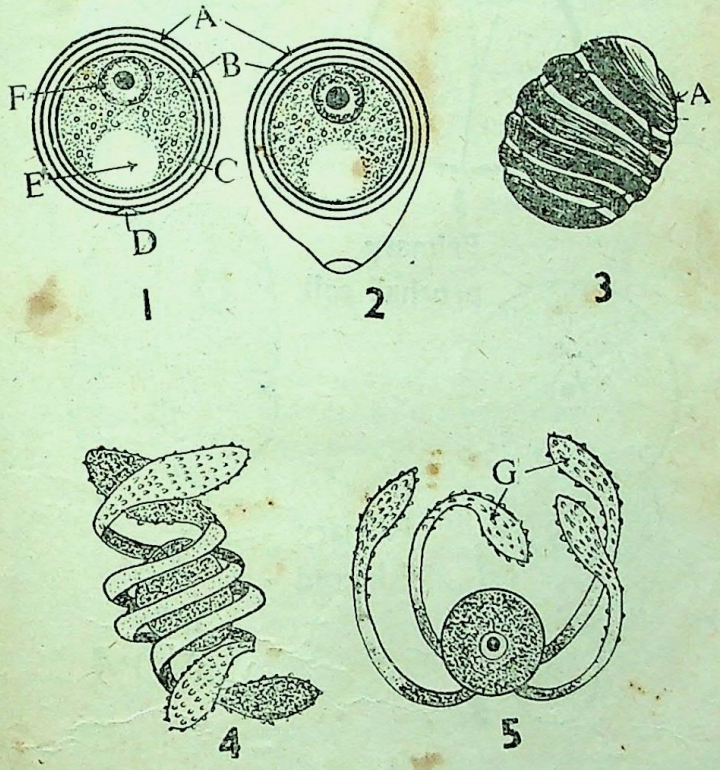

FIG. 53. Development of the spores of *E. limosum* 1, unripe spore with three coverings ; 2, Spore after lying 2—3, minutes in water ; The outer coat being detached ; 3, Beginning of the formation of elaters from the outer coat (perispore) ; 4, Perispore splits into spirally elaters which are coloured a beautiful blue by schultze solution ; 5, Spore in dry air (*A*, Outer colourless coat ; *B*, Light blue middle coat ; *C*, Inner yellow coat ; *D*, Point of attachment (umblical thickening) ; *E*. Vacuole ; *F*, Nucleus ; *G*, Elaters.

centrally placed nucleus and many chloroplasts. These remain viable only for a few days.

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The office of the elaters is to cause the following important functions.

(a) Their expansion results in the dehiscence of the sporangium.

(b) Their hygroscopic nature helps in the liberation of spores.

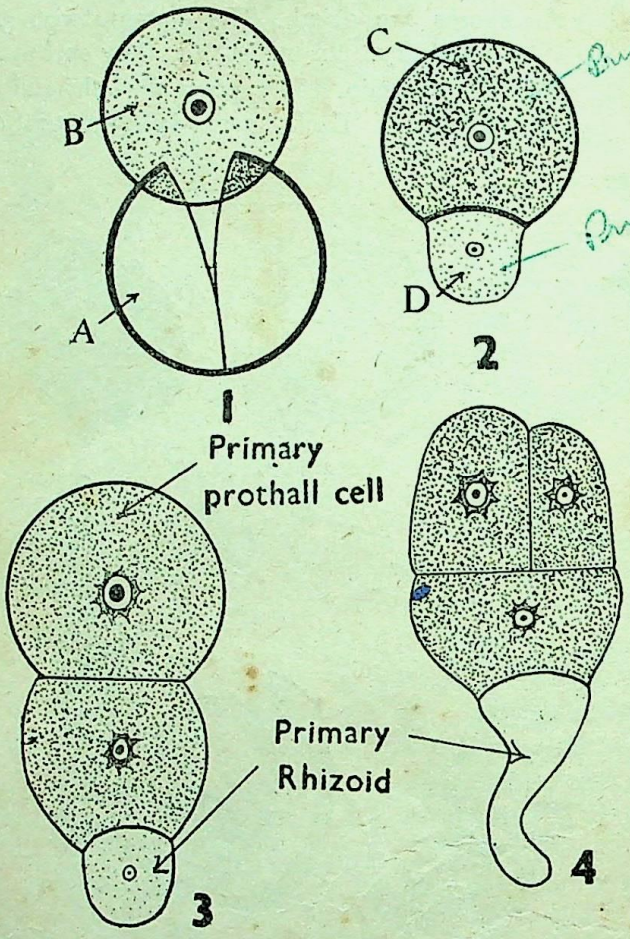

FIG. 54. Germination of spores of *E. arvense* and early development of gametophyte ; 1, Rupture of spore wall ; 2, Division of spore into an outer primary prothallial cell and an inner hyaline primary rhizoid cell ; 3-4, Later stages showing subsequent division of primary prothallial cell to form a filament of three cells (*A*, Exine ; *B*, Intine ; *C*, Primary prothallial cell ; *D*, Primary rhizoid cell.)

(c) They serve to keep the spores entangled together so that they are liberated in groups.

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Maclean and Ivimey Cook (1951) on careful observation found **two types** of spores. The **smaller** were much paler green than the **larger** ones but they were not in equal numbers nor was the number of each type constant in a tetrad. This case is interesting as it shows aparently an **early stage** in the development of **heterospory**.

Germination of Spore and Development of Gametophyte. The spores are delicate and remain alive only for a few days under favourable conditions they germinate at once and a small cell is cut off within 10 to 12 hours. The spores germinate rapidly in laboratory cultures on suitable media and on moist sphagnum. The spores lose their spherical shape. The chloroplasts disappear from the **smaller cell** which develops the first **rhizoid** (Fig. 54). The **larger cell** remains green and produces the gametophyte. The spore-wall soon gives way. The divisions which follow in the larger cell may be in any plane, thus there develops a flat plate of green tissue from which many filamentous branches are given out. The tissue is mostly one cell thick and there is no apical growth. This is the green peculiar **prothallus** of *Equisetum* which differs from that of on ordinary fern both in form and in the location of the sexual organs. When mature the prothallus consists of a disc shaped cushion several cells in thickness from the upper surface of which arise irregularly vertical erect **lobe-like** branches one cell in thickness, while the rhizoids arise from the lower surface. The prothallus grows in moist shaded habitats. The size of the gametophytes varies from a pinhead to eight mm. in diameter. The prothalli are extremely sensitive to such unfavourable environmental conditions as crowding, and their form is modified accordingly.

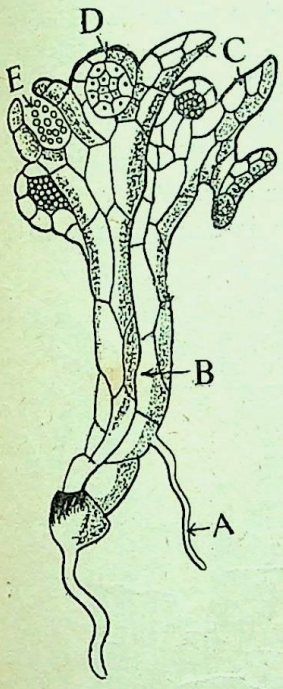

Fig 55. A male prothallium *E. arvense*. *A*, Rhizoid ; *B*, Gametophyte tissue ; *C*, Lobes ; *D*, Mature antheridium containing androgonial cells ; *E*, Ruptured antheridium containing spermatocytes.

The prothalli are of two types, **small male prothalli** which produce only antheridia (Fig. 55) and **large hermaphrodite prothalli** which produce antheridia and archegonia (Fig. 56). The question whether *Equisetum* is monoecious or dioecious is a controversial one. When the plant develops in fields they are generally **monoecious** *e.g. E. debile*, where archegonia develop first and antheridia later on, but when cultivated are

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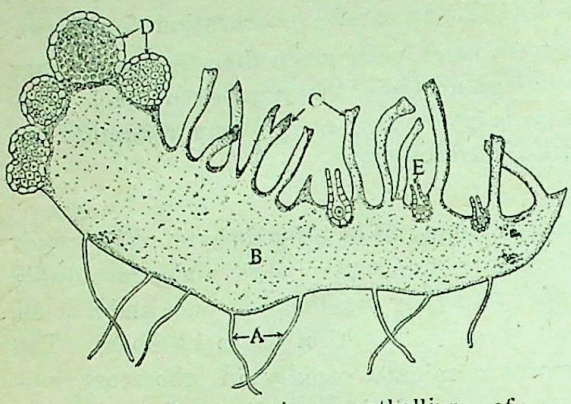

FIG. 56. A monoecious prothallium of *Equisetum* showing antheridia and archegonia. *A*, Rhizoids; *B*, Gametophytic tissue; *C*, Lobes; *D*, Antheridia; *E*, Archegonia.

dioecious due to unfavourable artificial conditions in which they are grown. *E. arvense* produces spores half of which develop male gametophyte and the rest half female. The male prothallus is small a few mm. long, deep red in colour and the lobes bearing the antheridia are more or less folded. Usually insufficiently fed prothalli develop male organs. The female prothallus is large about $\frac{1}{2}$" long and is green in colour (Fig. 57).

Development of the Archegonia. These develop on normal uncrowded prothalli when they are about a month or so old. The archegonia appear in the meristematic region where upright lobes are about to develop. At first the archegonia point downwards, but by subsequent development of fresh lobes, they become turned upwards. The archegonia arise from **superficial cells** which divide periclinally forming an outer **cover cell** and an inner **central cell** (Fig. 58). The former develops a few **neck cells** whereas the latter develops **primary canal cell** which develops two boat-shaped cells and a **primary venter cell** which forms an **egg** and a **venter canal cell**. The upper most neck cells are long and bend back, leaving a wide opening

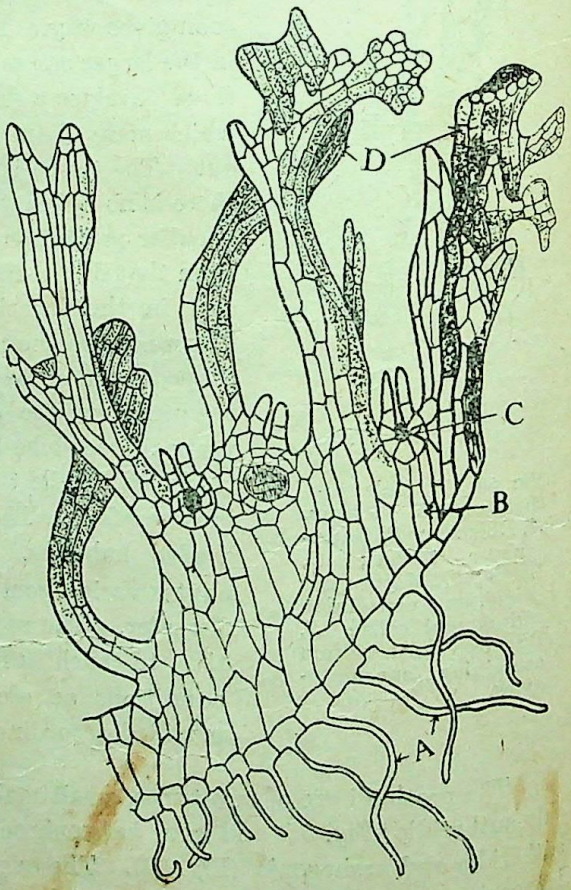

FIG. 57. Vertical section of a lobe of a strong female prothallium of E. *arvense* showing archegonia, *A*, Rhizoids; *B*, Gametophytic tissue; *C*, Archegonium; *D*, Lobes.

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for the entrance of the sperm. The archegonia lie either at the bases or between the lobes. As the gametophyte increases in size, additional archegonia may develop on the upper part of the thallus. When mature, an archegonium has a base sunken in the thallus and a short protruding neck. If the first archegonium is fertilized the gametophyte may cease to grow.

Development of Antheridia. These develop on normal uncrowded prothalli after the development of archegonia and on crowded starved

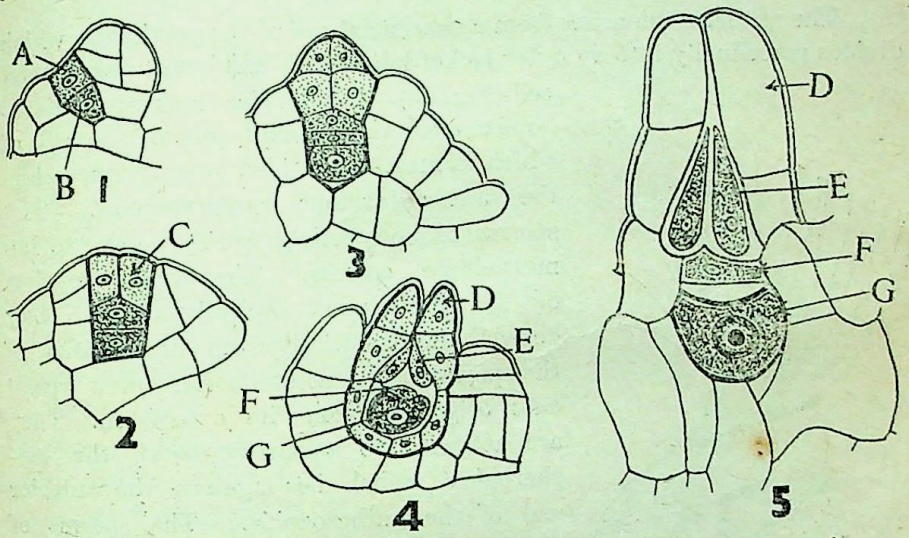

FIG. 58. Development of Archegonium of *Equisetum* 1, Division of superficial cell into an outer cover and an inner central cell; 2-3, Later stages; 4, Mature archegonium of *E. hyemale*; 5, Mature archegonium of *E. debile*. (*A*, Cover cell; *B*, Centre cell; *C*, Neck cell; *D*, Neck; *E*, Neck canal cell; *F*, Venter canal cell; *G*, Egg.)

prothalli when they are 20 to 30 days old. Usually they are developed

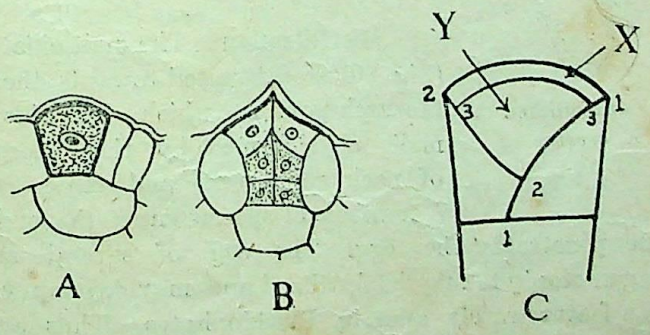

FIG. 59. Development of autheridium of *Equisetum*; *A*, Superficial cell; *B*, Division of superficial cell into jacket cells and androgonial cells; *C*, Pattern of the division of projecting type of antheridium. (*X*, Jacket initial; *Y*, Androgonial mother cell.)

in large numbers on the margin or apex of delicate lobes especially in

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those regions which are devoid of chlorophyll. The antheridia are of two types :

(a) **Sunken type**—formed on massive parts of plants.

(b) **Projecting type**—formed or the margin or apex of delicate lobes Generally the projecting type is rare but is a prominent feature of the dwarf plants (Fig. 59).

The antheridium arises from a **superficial cell** of the prothallus, which divides pereclinally into an outer **jacket initial** and an inner **androgonial cell** (Fig. 55). The former ultimately develops one cell thick **jacket**, (one of the cell of which forms a three sided operculum) while the latter develops **spermatocytes**. The spermatogenous cells geve rise to 100 to 150 multiciliate **sperms**. The sperm consists of an homogenous, spirally coiled body derived almost entirely from the nucleus of the spermatocyte, while its numerous apical cilia originate from its cytoplasm. They are attached to a narrow band, the **blepharoplast**, which lies against the anterior end of the antherozoids. The sperms of *Equisetum* are relatively large as compared to other Cryptogams. They are explosively discharged when the mature antheridia are moistened though a small opening in the outer wall.

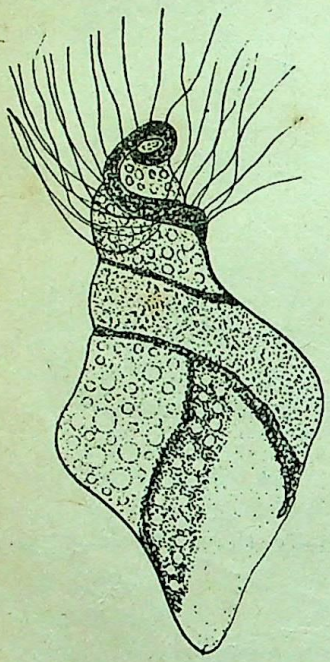

Fig. 60. Multiciliated sperm of *E. arvense*

Fertilization. The multiciliate sperms (Fig. 60) are attracted towards the neck of the archegonium which by this secretes malic acid formed by the disorganisation of neck canal cells and venter canal cell. A number of sperms enter the archegonium but only one penetrates the egg. The egg of several archegonia of a single gametophyte may be fertilized and may develop embryonic sporophytes, a feature rarely seen in Pteridophytes. Thus an oospore, marking the beginning of diploid sporophyte, is the result of fertilization.

Development of Embryo. The first division of the oospore, in most of the cases, is transverse and is followed by a division at right angles

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to the first. This four celled stage is **quandrant** stage of the embryo.

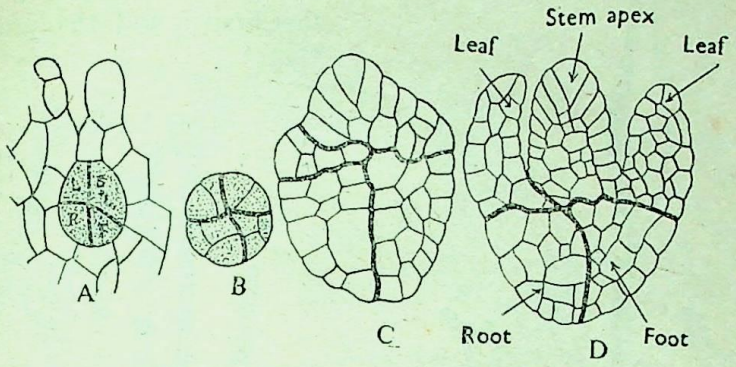

FIG. 61. *A—D*, Development of embryo of *Equisetum* (*L*, leaf ; *R*. Root ; *S*. stem ; *F*, foot)

From the upper epibasal half of the quadrant embryo, the larger cell forms the initial cells of the **stem** and the smaller those of the **leaf**. The larger cell of the hypobasal half forms, the **root** and the smaller cell a weak **foot**. No suspensor is formed and the entire structure becomes the embryo proper (Fig. 61).

Very early in the development the apical cells of stem and primary root are organised (Fig. 62). Due to rapid growth, the embryonic root bursts through the tissues of the gametophyte into the soil, thus establishing the independence of the young sporophyte.

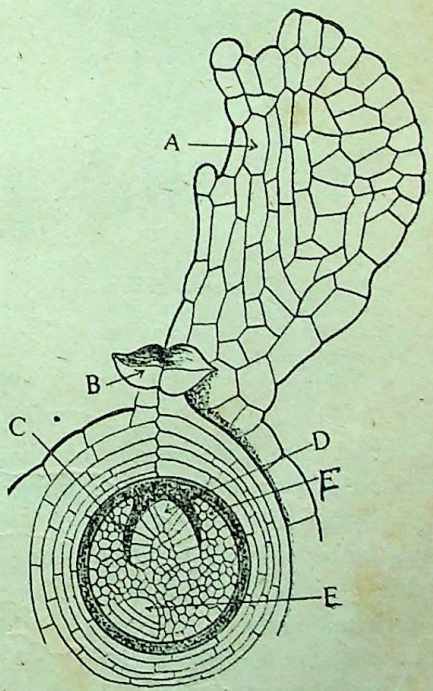

FIG. 62. Mature embryo of *E. arvense* imbeded in the prothallus *A*, Prothallial tissue ; *B*, Neck ; *C*, Leaf ; *D*, Stem ; *E*, Root. *F*-Leaf.

The stem portion of the embryo bursts through the neck of the archegonium, which forms the **calyptra**, and grows upright. The primary stem grows straight until it has differentiated into a dozen nodes, each of

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which bears three leaf-teeth. Soon a more vigrous branch arises from the base of this primary stem, and this in turn is replaced by another branch and the process is repeated. The third or fourth of this series of branches which enter the soil and remain underground form the rhizome of the mature or adult plant. During the course of development, the primary root withers and its function is taken up by adventitious roots which develop from the base of the stem. Thus the embryo develops into a young sporophytic plant body, whose stem is differentiated into nodes and internodes with a whorl of scale leaves at each node and an underground rhizome with unlimited growth. Mention must be made of the primary (embryonic) stem which is peculiar in that it shows a protostelic solid structure with well developed xylem without any carinal canals. The seedling shows a **protostelic** structure but at the level of the first branch a **siphonostelic** structure is revealed. This structure persists at the nodes in the adult plant whereas the internodes show a **eustelic** or polyfascicular siphnostelic structure.

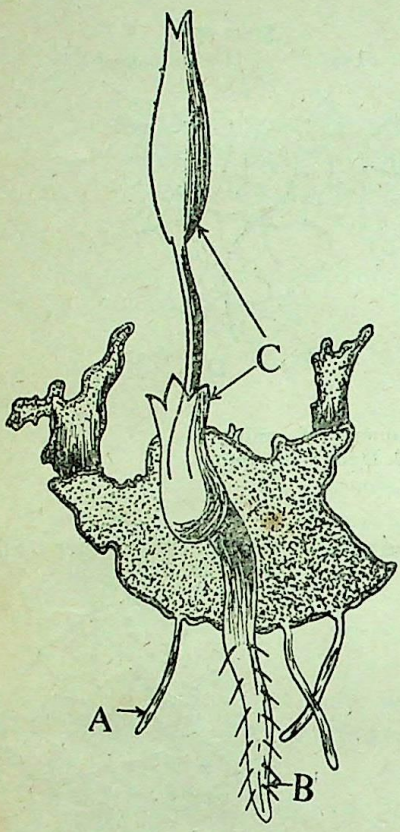

FIG. 63. *E, arvense* Vertical section of a lobe of a prothallus with a young sporophyte *A*, Rhizoids ; *B*, Root ; *G*, leaf sheaths.

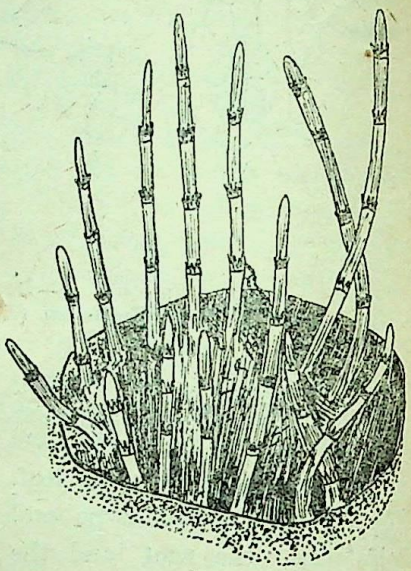

FIG. 64. A large prothallus of *E. debile* with fifteen young sporophytic plants.

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Economic Importance.

The species of *Equisetum* are not of much importance today

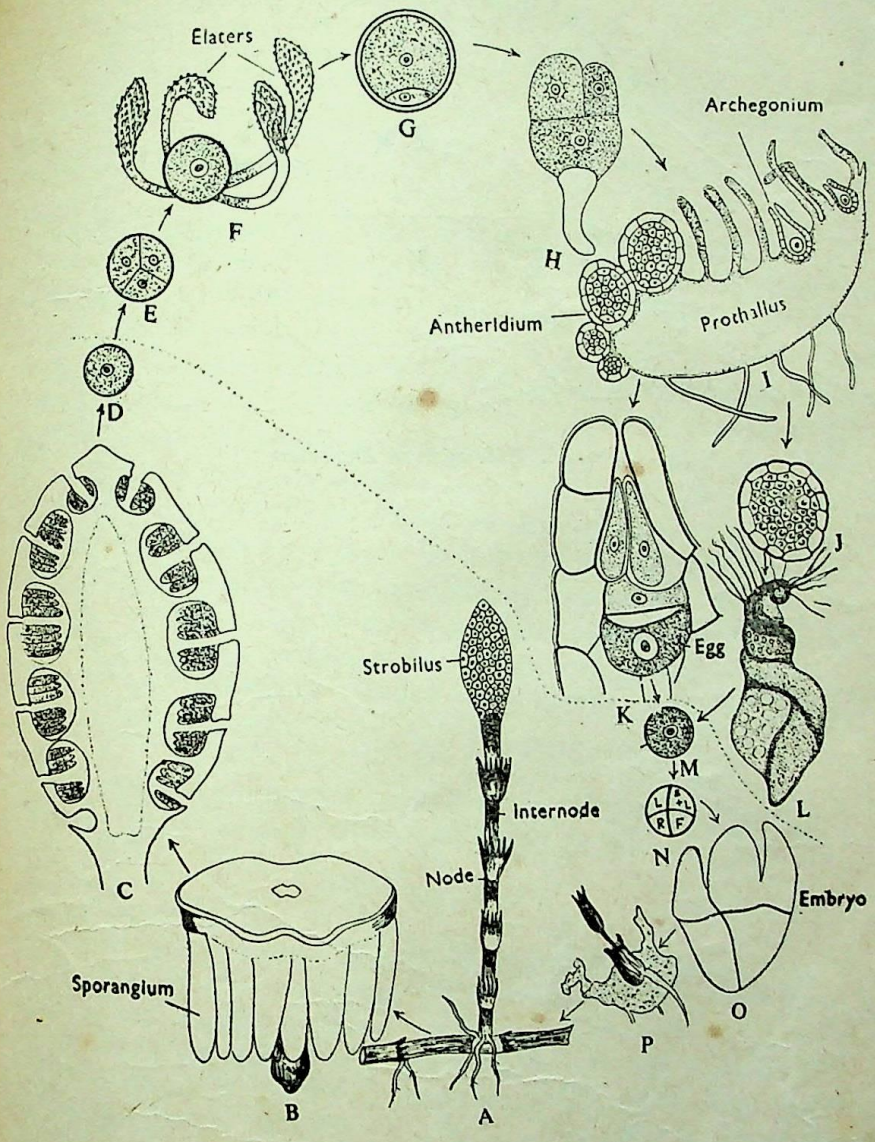

FIG. 65. Diagrammatic representation of the life history of *Equisetum A*, sporophytic plant ; *B*, A sporangiophore with pendant sporangia ; *C*, L. s. of strobilus ; *D*, Spore mother cell (2x) ; *E* Tetrad of spores (x) ; *F*, Spore with elaters ; *C*, *H*, Development of gametophyte ; *I*, Mature prothallus with antheridia and archegonia ; *J*, An antheridium ; *K*, An archegonium ; *L*, Sperm ; *M*, An egg ; *N*, Oospore ; *O*. Embryo ; *P*, Young sporophyte.

but in the days gone by they were used for scouring pewter dishes

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and for polishing wood. *E. debile* is given as a cooling medicine sometimes for gonorrhoea.

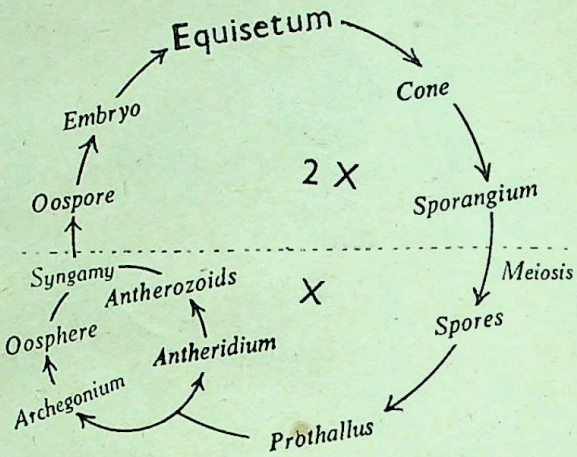

FIG. 66. Life cycle of *Equisetum*

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CHAPTER 9

PTEROPSIDA

The Pteropsida is the largest and most important of the plant groups as it includes three classes : Filicineae, Gymnospermae and Angiospermae. Its fossil history does not go beyond the Devonian. The present day members are all **megaphyllous** in habit. The megaphyl- a[ns] leaves are usually markedly larger (but not always), than the micro- the[llous] leaves and are distinguished by the presence of branched veins "spo[r] blades and of parenchymatous gaps in case of siphnostelic stems [the] point of departure of their leaf-traces. The group is highly [d] on account of the diverse structural and functional modifica- [he] megaphylls which result in a great variety of forms. The [ls] a variable stele structure ranging from the simplest **protostele** [de]veloped siphnosteles and **dictyosteles.** The sporangia [el]oped in an eusporangiate or leptosporangiate manner are [upon] the **abaxial** surfaces of the leaves. These may or may [mo]difications.

[F]or sake of convenience, we have used **Pteropsida** in a restrict- [ov]er the **megaphyllous pteridophytes** only.

FILICNEAE

[The] history of this class can be traced to remote geological [th]ey formed an insignificant vegetation in the Carbonifer- [ou]s son to Lycopodineae and Equisetineae. A good many [fo]rms living today can be traced back to the Triassic and [th]e Mesozoic period. A total number of about 215 genera [an]d species are included in the class Filicineae. They are world- [di]stribution, thriving in wide variety of habitats. In majority [of] the leaf seems to have become the dominant organ of the [pl]ant, whereas the stems are correspondingly inconspicuous. [In] they are abundant in the tropical damp mountain forests [with] dense vegetation on its floor. They show a great diversity in [ha]bit. Some of the genera are **hydrophytes** such as *Azolla, Salvinia* and [*Ma*]*silea*; a few are **halophytes** such as *Acrostichum* ; most of them be- [ar] rhizome or less as **xerophytes** such as *Adiantum, Polypodium* and a few [fo]rms in cer[tain]

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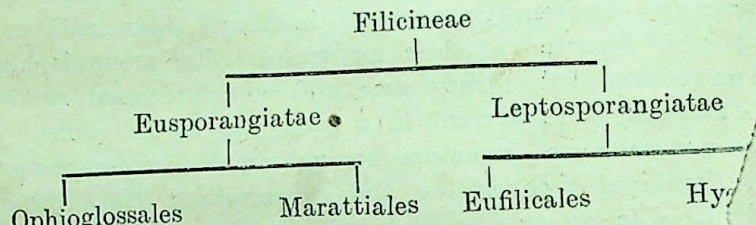
others are **epiphytic** like *Asplenium* etc. Whatever their habit may be the sporophyte is **perrennial**.

Classification. Bower (1923-1926) on the position of the sporangia on the sporophyll divided the ferns into two series : **Marginales,** where the sporangia are marginal in position such as *Pteridium, Pteris* etc. and **Superficiales** where the sporangia are arranged on the lower surface such as *Polypodium, Marattia* and *Dryopteris*. On the basis of the development of sporangia, Bower divided the ferns in three groups : **Simplices** where all the sporangia develop at the same time such as Osmundaceae, Schizeaceae ; **Mixtae**—where sporangia develop in an irregular manner such as Polypodiaceae ; and **Gradatae**—where sporangia develop in basipetal succession such as in Cyatheaceae and Hymenophyllaceae.

Engler and Diels (1936) divided the Filicineae into **Eusporangiatae** and **Leptosporongiate** and these are further divided as follows :—



Eames (1936) and Arnold (1947) have divided the F
four orders : **Filicales, Marattiales, Ophioglossales** and **Coe**

FILICALES

These are commonly known as the "true ferns" and a
by a total number of 200 genera and 8,700 species. The
the characteristic features of this order :

1. The wall of the sporangium is one cell in thickne
2. The sporangium originates from a single superfic
3. Early differentiation of the tapetum.
4. Small projecting antheridia.
5. Formation of uniform quardants in the formation of e
6. Circinate vernation of leaves.

According to Smith (1936) the Filicales have been divide
families : Marsileaceae, Salviniaceae, Polypodiaceae, Dick
Cyatheaceae, Hymenophyllaceae, Gleicheniaceae, Schizaeac
Osmundaceae.

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be, the leaves are compound and the leaf-blade is divided into four equal obcuneate pinnae. Thus the leaf has four leaflets in a terminal cluster resembling a four leaved clover. Actually the four leaflets do not arise at one locus from the petiole, but two are slightly higher than the others and are inserted in an alternate fashion. Each leaflet shows repeated dichotomously branched venation. The veinlets are connected with marginal loops and cross connections thus forming a net work. Puri and Garg (1953) have suggested that the so-called leaf of *Marsilea* consists of **single leaflet** which in turn bears four **pinnules.** Usually these pinnules have been referred as leaflets in most of the books. Sometimes, the pinnae may be once or twice deeply lobed dichotomously as in *M. macrocarpa* and *M. biloba* or may become coarsely toothed as in *M. minuta*. At night the pinnae of the aerial leaves commonly assume a sleeping position, being folded upwards, as in bud. Near the base of the petiole are situated stalked bean shaped green structures—the **"sporocarps"** (Fig. 67).

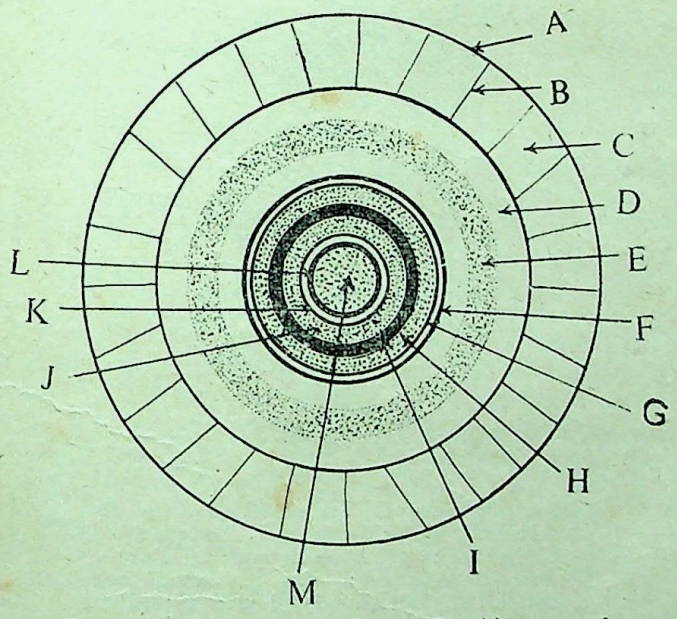

FIG. 68. Diagrammatic T. s of rhizome of *Marsilea* showing amphiphloic siphonostele (*A*, Epidermis ; *B*, Septum ; *C*, Aerenchyma ; *D*, Parenchymatous cortex ; *E*, Sclerenchymatous cortex ; *F*, Outer endodermis ; *G*, Outer pericycle *H*, Outer phloem ; *I*, Xylem ; *J*, Inner phloem ; *K*, Inner pericycle , *L*, Inner endodermis ; *M*, Pith).

Root. The roots arise from the nodes on the underside of the rhizome either singly or in groups. They are of **adventitious** type. These in certain abnormal cases, may develop from internodes (Fig. 67).

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Internal Structure :

Stem or Rhizome. The young stem shows a **protostelic** structure, others solid xylem is completely surrounded by phloem. But as it becomes old pith begins to appear in the centre. Gradually, internal phloem, internal pericycle, and internal endodermis develop. This peculiar structure is called **amphiphloic siphonostele** (Fig. 68, 69). In

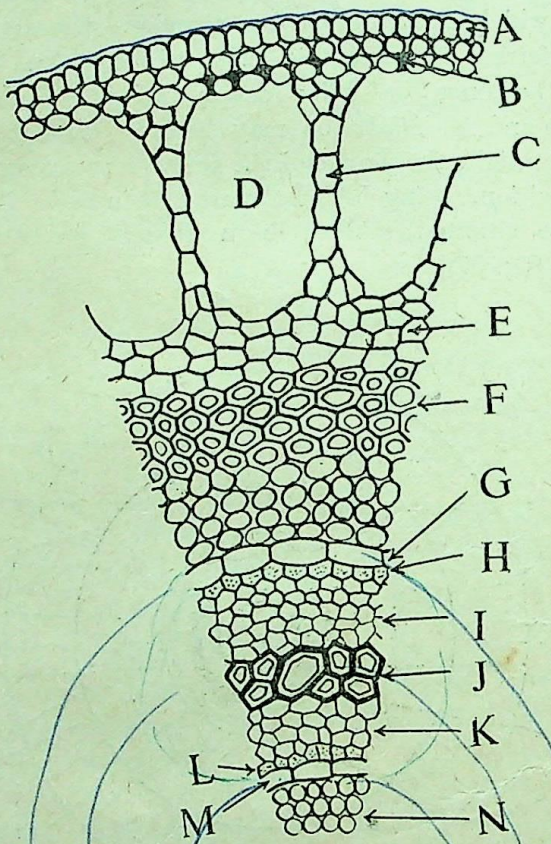

FIG 69. Part of T. s. of *M. quadrifoliata* rhizome. (*A*, Epidermis ; *B*, Tannin cell ; *C*, Septum ; *D*, Aerenchyma ; *E*, Parenchymatous cortex ; *F*, Sclerenchymatous cortex ; *G*, Outer endodermis ; *H*, Outer pericycle ; *I*, Outer phloem ; *J*, Xylem ; *K*, Inner phloem ; *L*, Inner pericycle ; *M*, Inner endodermis ; *N*, Pith).

certain cases, the protoxylem is well difined, as is seen in *M. vestita*, but in other cases such as *M quadrifoliata* it is not well defined. The structure of the pith depends upon environmental conditions. If the plant is submerged, the pith is parenchymatous, if rooted in mud, the pith is more or less sclerotic. The inner portion of the cortex is a solid tissue of thin walled or scletotic parenchym. Outside this is present an air storage tissue with a single row of air chambers. This is called

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aerenchyma. The outer-most portion of the cortex is a parenchymatous tissue, one to several cells in thickness. This is bounded by a single-layered **epidermis** without any stomata.

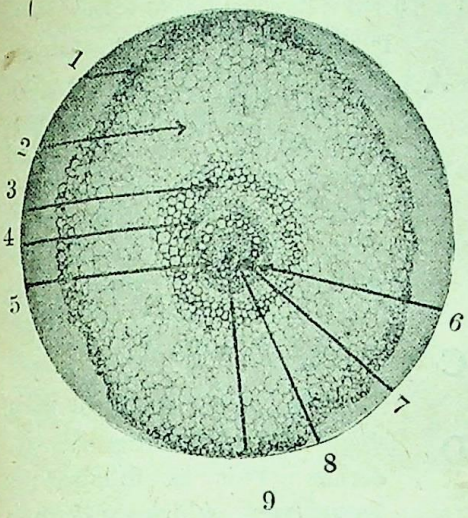

FIG. 70. Photomicrograph of rhizome of *Marsilea sp.* (1, Epidermis) 2, Aerenchyma; 3, Scl. cortex; 4, Outer endodermis; 5, Xylem; 6, Outer phloem; 7, Inner phloem; 8, Inner endodermis; 9, Pith.)

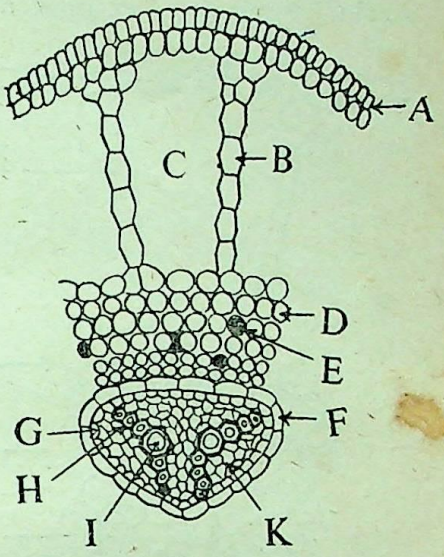

FIG. 71. Part of T. s. of Petiole *Marsilea sp.* (*A*, Epidermis; *B*, Septum; *C*, Aerenchyma; *D*, Parenchymatous cortex; E. Tannin cell; *F*, Endodermis; *G*, Pericycle; *H*, Protoxylem; *I*, Metaxylem; *K*, Phloem.)

Petiole. It displays a **protostelic** structure. The single centrally placed stele is triangular in outline, as revealed by a transverse section (Fig. 71). The petiole is traversed by a **"V"-shaped** vascular trace which leaves a gap above the place of its departure from the stem stele. It is bounded bp a single layer of **endodermis**. The xylem is "V"-shaped, each arm of which is composed of larger tracheids representing the protoxylem at either end pointing its exarch nature. The opening of 'V' is always towards the axis. The 'V'-shaped xylem is surrounded by phloem and pericycle. The structure of the cortex is similar to that of the stem.

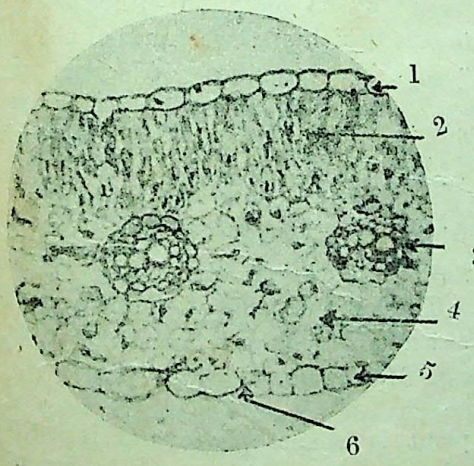

FIG. 72. Photomicrograph of a part of T. s. of leafblade of *Marsilea sp.* (1 Epidermis; 2, Palisade; 3, Concentric amphicribral bundle; 4, Spongy tissue; 5, Lower epidermis; 6, Stoma.)

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Pinna or **leaflet.** A transverse section reveals that the **mesophyll** is bounded by upper and lower **epidermis** ; in aquatic forms with floating leaves, the **stomata** are confined on the upper epidermis but in case of amphibious plants, they are seen on both the surfaces. Whatever their position may be the stomata are slightly sunken (Fig. 72). The mesophyll is very well differentiated into elongated upper **palisade** and lower rounded **spongy** cells, with large capacious air-spaces bounded by the septa. The vascular bundles are concentric and of amphicribral type.

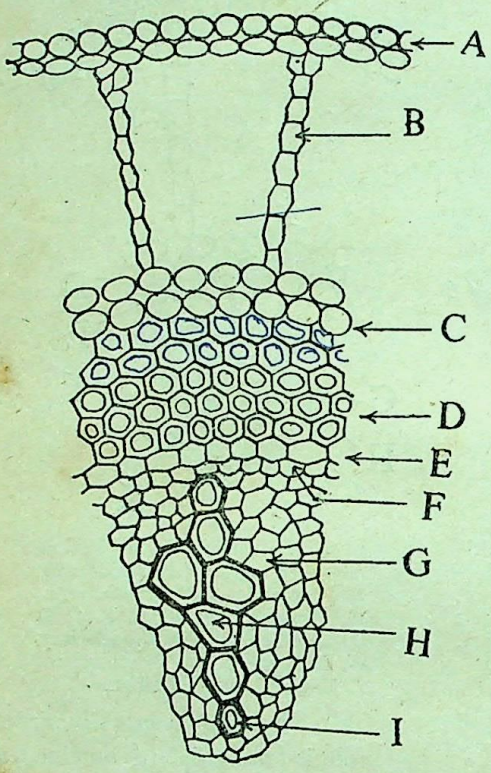

FIG. 73 Part of T. s. of *M. quadrifolia* root showing a diarch stele. (*A*, Epidermis; *B*, Septum; *C*, Parenchymatous cortex; *D*, Sclerenchymatous cortex ; E, Endodermis ; *F*, Pericycle; *G*, Phloem ; *H*, Metaxylem; *I*, Protoxylem)

Root. It is bounded by a single-layered continuous **epidermis**. This is followed by **aerenchyma**, which in turn is followed by compact parenchymatous or sclerenchymatous cells, finally bounding the stele by a single layered **endodermis** (Fig. 73). The **protostele** shows a typical **diarch** structure with a centrally diametrically placed xylem plate on either side of which are two bands of phloem. The bundles of xylem and phloem are radially arranged and are surrounded by a single layer of **pericycle**.

Vegetative Propagation. During dry period, certain branches develop from the rhizome. These swell up due to the storage of food material and are called **tubers.** These are capable of tiding over unfavourable periods and on the return of favourable conditions, they germinate to develop a new plant *e.g.*, *M. hirsuta.*

Sexual Reproduction. The plant is a sporophyte and is **heterosporous.** It is different from other ferns, because the sporangia are not developed on leaves, but on special structures—the **sporocarps.**

Sporocarp. These are flat bean-shaped structures soft and green in the beginning but become hard and brown at maturity. They appear after a long period of vegetative development. The sporocarps are borne

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on a short or long stalk either singly or in clusters depending on the species. They occur on short lateral branches of the petiole. Their attachment in different species is different. The number of sporocarps on the leaf varies with the species. In most cases, there is a single sporocarp while in others like *M. caribaea* and *M, quadrifolia* the number may range from two to twenty or even more. When numerous, they are arranged in a row, one above the other.

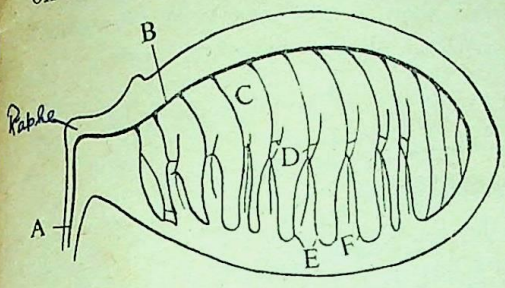

FIG. 74. Vascular supply of the sporocarp of *M. quadrifolia*. *A*, Stalk bundle; *B*, Dorsal bundle; *C*, Lateral bundle; *D*-E, Placental bundle; *F*, Fork of lateral bundle.

The sporocarp is a biconvex somewhat flattened structure. Near the point of attachment of the stalk one or more protuberances are seen in the median plane. These are called **tubercles**. The end of the stalk which is fused laterally to the back of the sporocarp is called **raphe.**

The vascular supply of the sporocarp consists of a **main vein** along the narrow side facing the peduncle, from which are given off alternately right and left dichotomously-branched **lateral veins** at right angles to the median vein (Fig. 74). A **receptacle** develops at the region where each lateral vein forks. Receptacles on one half of the sporocarp alternate with those on the opposite half. A flap like outgrowth two cells in thickness develops in a hood like manner over the entire receptacle. Each receptacle projects inwards from the wall.

The sporocarps are very hard, with a **thick wall** strongly resistant to mechanical injury and to drying out. The remarkable longivity and the resisting powers of the sporocarp which deserve mention are due to its wall. Sporocarps from herbarium sheets after fifty years and others kept in alcohol have resumed activity when placed in water.

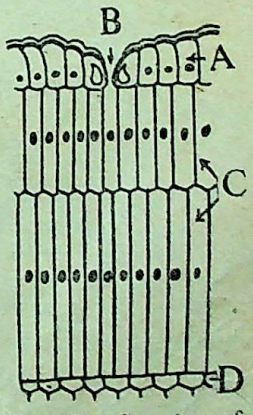

FIG. 75. Structure of the wall of sporocarp *A*, Epidermis; *B*, Stoma; *C*, Priosmatic cells; *D*, Gelatinous cells)

Internal Structure of the Sporocarp.

Dorsoventral Section—The sporocarp, when cut dorsoventrally reveals an outer **epidermis** formed of broad, columnar cells with stomata. Below this lies a layer two to three cells thick, formed of thick-walled elongated brick-shaped cells (Fig. 75). These lie at right angles to the epidermis and are responsible for providing mechanical strength to the wall. These cells are known as **priosmatic cells** and are followed by a layer

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of **gelatinous tissue**. The sporocarp seems to be a modified leaf or blades enclosing a group of sori. Each sorus is formed in a cavity that extends dorsiventrally and the latter is lined with a delicate **indusium** completely

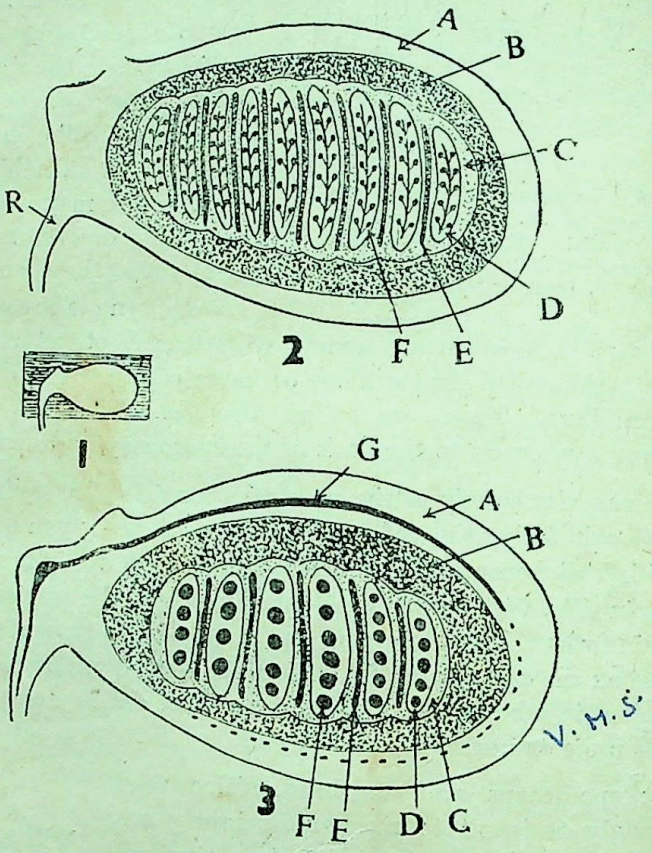

FIG. 76. I. (1-2-3) Internal structure of sporocarp of *Marsilea*. 1. Plane in which the dorsoventral section is cut ; 2, Section cut somewhat to one side of the median line, showing microsporangia ; 3, Slightly farther away from 2, showing megasporangia. (*A*, Sporocarp wall ; *B*, Gelatinous ring ; *C*, Cytoplasm ; *D*, Sorus ; *E*, Indusium ; *F*, Microsporangia ; *F*, Megasporangia ; *G*, Lateral branch ; *H*, Placentral branch ; *I*, Tubercle ; *R*, Raphe)

investing the sorus which contains **micro**–and **megasporangia** (Fig 76 *2-3*). The receptacle of the sorus is ridge-like and bears along its top, a row of megasporangia and around its sides many microsporangia. Thus the sporocarp shows two rows of **chambers** which alternate with one another and run from above downwards.

Transverse Section—Here only two chambers of sori surrounded by its indusium are seen. Each sorus contains a receptacle which possesses only one kind of sporangia either male or female (Fig. 76-7).

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Longitudinal Section—Here there are two alternating rows of sori, each of which is surrounded by a two-layered indusium (Fig. 76-5). The

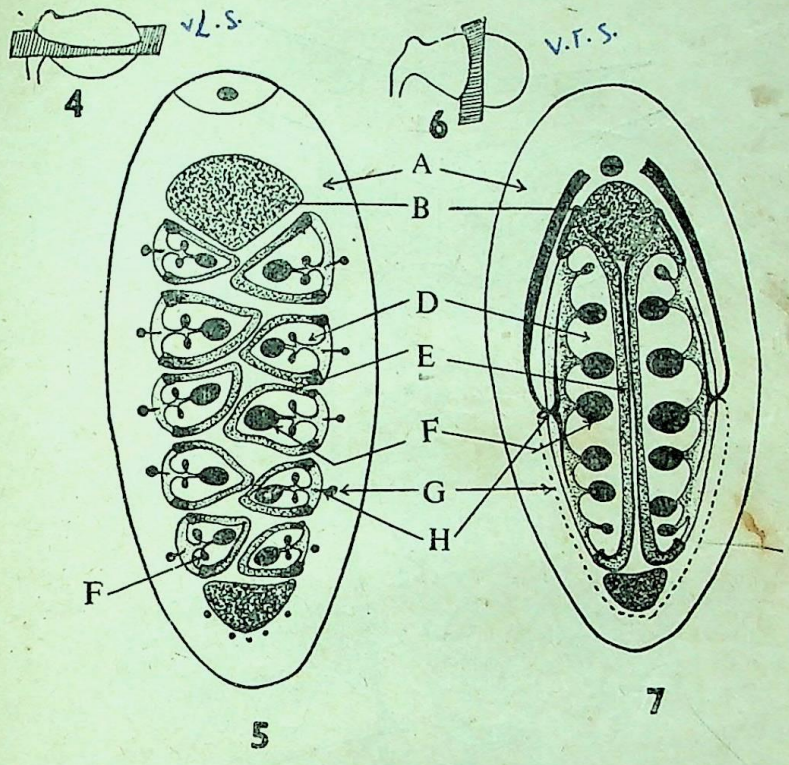

FIG. 76. II (4-7) Internal structure of sporocarp of *Marsilea*
4, Plane in which longitudinal section is cut ; *5*, Longitudinal section ; *6*, Plane in which T. s. is cut ; 7, Transverse section.

receptacle possesses a single terminal megasporangium and the microsporangia are laterally arranged on the sides. There is only one megaspore in the megasporangium whereas the microsporangium contains many microspores.

Morphological Nature of the Sporocarp—Two hypothesis have been advanced to account for the morphological nature of the sporocarp. According to **Laminar hypothesis** (Fig. 77) put forth by Bower, Eames, Puri and Garg, the sporocarp is regarded as a **modified fertile segment** from the lower part of the leaf. The **Petiolar hypothesis** of Johnson considers it to be **homologous with the swollen end of the petiole** only of the sterile branch of the leaf, in which the marginal cells are developed to the formation of the sporangia instead of lamina. This is supported by the fact that the apical growth of the sporocarp resembles that of an entire leaf rather than that of a pinna.

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The laminar hypothesis is supported by many facts and hence seems to be very correct. According to Goebel, the nature of the vascular

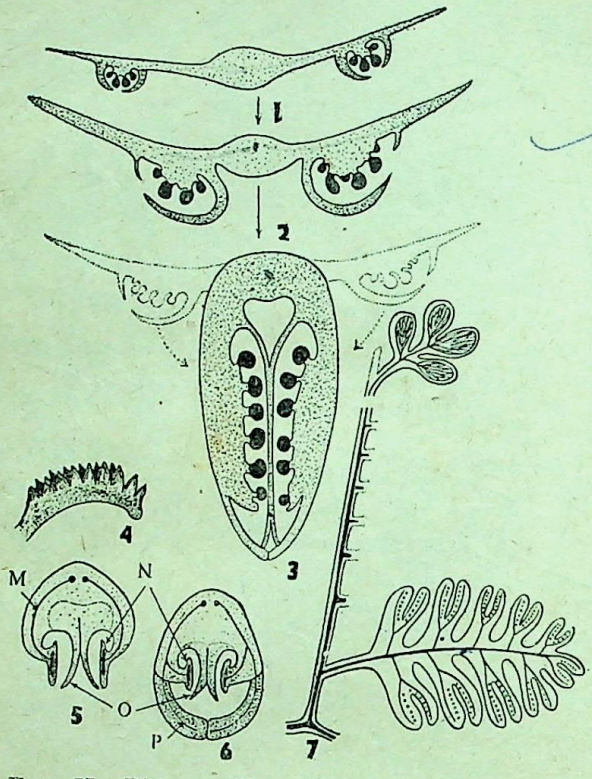

FIG. 77. Diagrams illustrating morphological nature of sporocarp. 1–3 Diagrams suggesting evolution of sporocarp by an enfolding of pinnule of Cyatheaceous leaf (*Smith's view*) ; 4, Portion of young fertile leaf of Schizea with the pinnae reflexed to the abaxial side (*Bower's view*) ; 5–6, *Eam's view* ; 5, Sori partly enclosed by indusia facing inwards ; 6, Wing like shoulders developed which are curled downwards and inwards until they meet enclosing the sori ; 7, *Puri* and *Garg's* view.

supply to the peduncle and the vascular system within the sporocarp seems to show that it is a **leaf pinna.** Busgen, variously interprets the sporocarp as **resulting from an apposition of the two pinnae or from an enfolding of a single pinna.** But this view is further subjected to the criticism that the single bundle in the peduncle and the single mid-vein of the sporocarp show that it is not a pair of pinnae. This view has been supported by Bower and Campbell. They consider the pinna to be a pinnately divided structure in which the pinnules have fused with one another and the sporocarp has developed from an enfolding of the pinna. This condition is seen in a fern **Schizea.** The sporocarp, therefore, is regarded as **"a lateral fertile modified segment."** According to Puri and Garg (1953) **"The sporocarp is equivalent to a single leaflet which consists**

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of as many pinnules as the number of commissural bundles (lateral bundles), the latter forming the mid-rib of the former".

But the exact position of protoxylem in a leaftrace and petiole, pointing close similarity with the vascular bundle of the sporocarp,

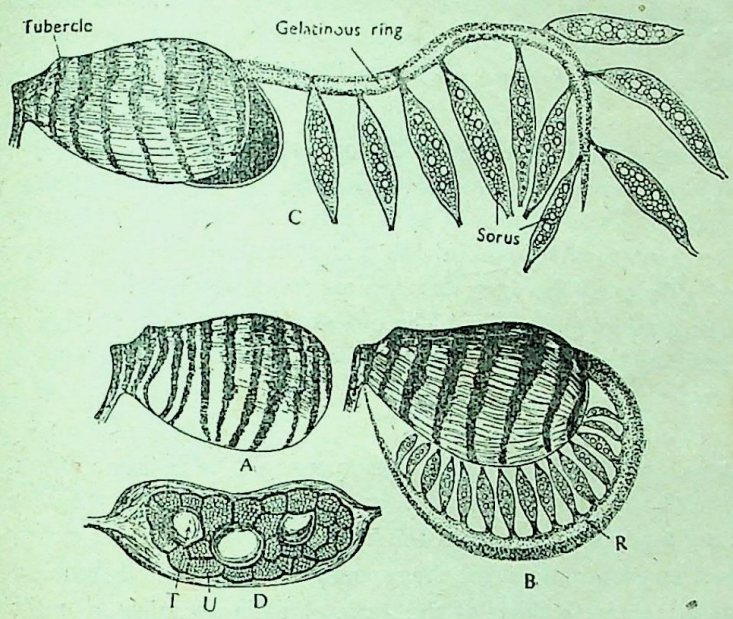

FIG. 78. Bursting of sporocarp and liberation of sori of *Marsilea*. *A*, Sporocarp ; *B–C*, Stages in bursting and extrusion of gelatinous ring ; *D*, A soris containing micro and megasporangia enclosed by indusium. (*R*, Gelatinous ring sporophore) *T*, Megasporangium *U*, Microsporangium)

suggest that the sporocarp of *Marsilea* is more like an **enfolded pinna of the cyathiaceae** than an enfolded pinna of Schiziaceae. Its cyathiaceous nature is further supported by the **gradate sorus, by the enclosure of the receptacle by an indusium** and **by the occurrence of ten to fifteen sporangia in longitudinal series.**

Bursting of Sporocarp and Liberation of Sori. In nature probably bacterial action plays a role in rotting the sporocarp wall and thus effecting spore liberation (Fig. 78). The sporocarp opens only in water. The splitting takes place in a bivalve-like manner along the ventral side and apex. A ring of gelatinous tissue, which extends around the cavity in the dorsoventral plane, absorbs water. This causes a great expansion of the gelatinous tissue *i.e.*, **sporophore,** which protudes along the open margin of the sporocarp. As it does so, it drags the sori, which are attached to it by their ends. The sporophore bears two rows of **soral sacs,** one on either side, alternating with one another. These are freed from

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the wall of the sporocarp by abcission below the receptacle. The dorsal segment elongates greatly and the ring becomes a worm-like structure, attached by one end of the sporocarp, with two rows of soral-sacs extending from one side. The ventral end is weak and soon degenerates. The ventral ends of the sori are torn open when freed from the ring and part of the spores of each sorus atonce escapes from the open end. The delicate mucilagenous sporangial walls break open and the spores are liberated, which germinate at once.

Development of Sporangia. According to Marshall (1925) both the micro and megasporangia develop according to **leptosporangiate** method. **Sporangial initials** develop first at the apex of each ridge-like receptacle and subsequently, additional initials on the flanks initiate sporangium development. Those at the apex develop megasporangia while the lower ones develop into microsporangia. The oldest sporangia are at the apex and the younger at the base of the receptacle. This is known as **gradate condition.**

Development of micro and megasporangia is alike upto the stage where each has a jacket one cell in thickness without any **annulus**, a nourishing **tapetum** two cells in thickness, and between 32 to 64 **spores.** In case of megasporangia, all the spores except one degenerate Their contents mingle with those of the tapetal cells forming a multinucleate **plasmodium.** The functional megaspore, as a result of the absorption of large quantities of food material, increases to many times its original size and becomes somewhat ellipsoidal. All the spores in the microsporangium are functional. The microspores are many times smaller than the megaspores and are arranged in tetards, hence show a faint triradiate ridge. Unlike those of *Selaginella*, the spores of *Marsilea* do not germinate until they have been shed from the sporocarp.

Microspore and Development of Male Gametophyte. A microspore is globose in shape and is surrounded by a thick outer wall consisting of the outermost transparent **epispore** and **exospore**, and a delicate thin endospore. It has a singlecentral nucleus and dense cytoplasm containing starch grains. The spores germinate at once when set free, At room temperature, the microspores germinate in about one hour and sperms are liberated in 10 to 12 hours (Fig. 79).

The first evident change in germination of a spore is the migration of the starch grains to the periphery. The male gametophyte is similar to that of an heterosporous fern. First of all, there is cut off a single small **prothallial cell** (Fig. 79 *C*) but Belajeff has shown **two** prothallial

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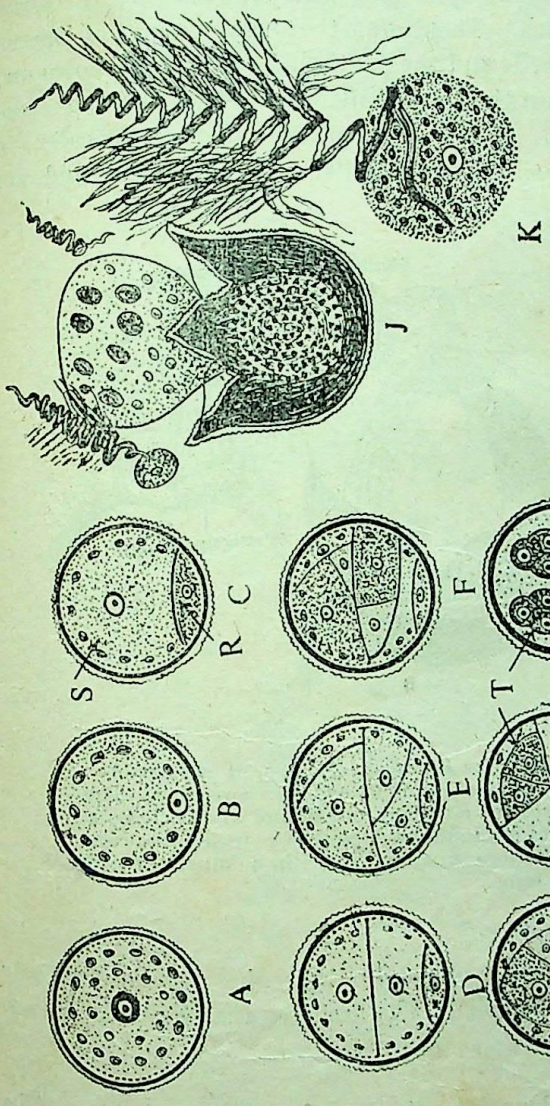

FIG. 79. Microspore and development of male gametophyte (*A—K*) (*A*, Microspore at the time of liberation from sporocarp ; *B*, Preparing for germination ; *C*, Division of microspore into a small prothallial cell and a large apical cell ; *D*, Division of apical cell into two antheridial initials ; *E-F*, later stages showing formation of jacket ; *G*, Formation of two primary androgonial cells; *H-I*, Formation of androcytes; *J*, Ruptured microspore showing liberation of sperms from the protruded endospore ; *K*, A single multiciliated sperm. (*R*, Proth. cell, *S*, Apical cell ; *U*, Primary androgonial cell ; *T*, Androcytes)

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cells in *M. quadrifolia*. The next (Fig. 79D) divides the large apical cell equatorially and each of the cell so formed is apparently an **antheridium initial.** In each initial there is cut off, on one side, a large **wall cell**, by a periclinal wall (Fig. 79E). A small cell is then cut off by wall (Fig. 79F) internal to this, along the median wall. Another periclinal division (Fig. 79G) completes a **jacket** of external cells around two inner cells. These two inner cells, are the two **spermatogenous cells** and by successive division, each forms 16 **sperms**. Therefore, the total output of sperms is 32. Later on the jacket cells and the prothallial cells break down and the spermatocytes float within the spore wall. By bursting of the spore wall the sperms are liberated. The sperms of *Marsilea* are peculiar in that they have many more coils, sometimes like a dozen or more and are

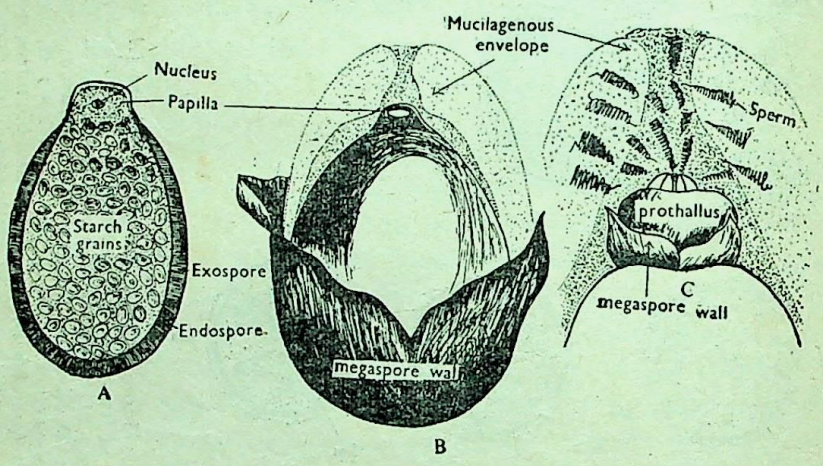

FIG. 80. Megaspore of *Marsilea salvatrix*. *A*, L. s. of megaspore; *B*, Megaspore with its surrounding mucilagenous envelope. The apical papilla projects into the mucilagenous funnel and encloses a broad yellowish drop; *C*, Prothallium projecting from the ruptured wall of the megaspore surrounded with a mucliagenous funnel with numerous sperms.

cork-screw like in form. They are unusual in that the flagella are only attached to the broad posterior coils. The first few anterior coils do not possess any cilia.

Megaspore and Development of Female Gametophyte. The megaspores are ellipsoidal with a small rounded protuberance at the anterior pole (Fig 80). They are sufficiently large to be readily visible to the naked eye. The mucilagenous spore wall about the protuberant portion is relatively thin and on it the triradiate ridge remains visible. The spore wall is much thicker and shining except this region. The nucleus lies in the dark-coloured anterior protuberant

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apical portion having dense grannular cytoplasm. The remaining **basal** protoplastm contains numerous large starch grains, oils, albuminous matter, embedded in a watery cytoplasm. Development of the female gameto-

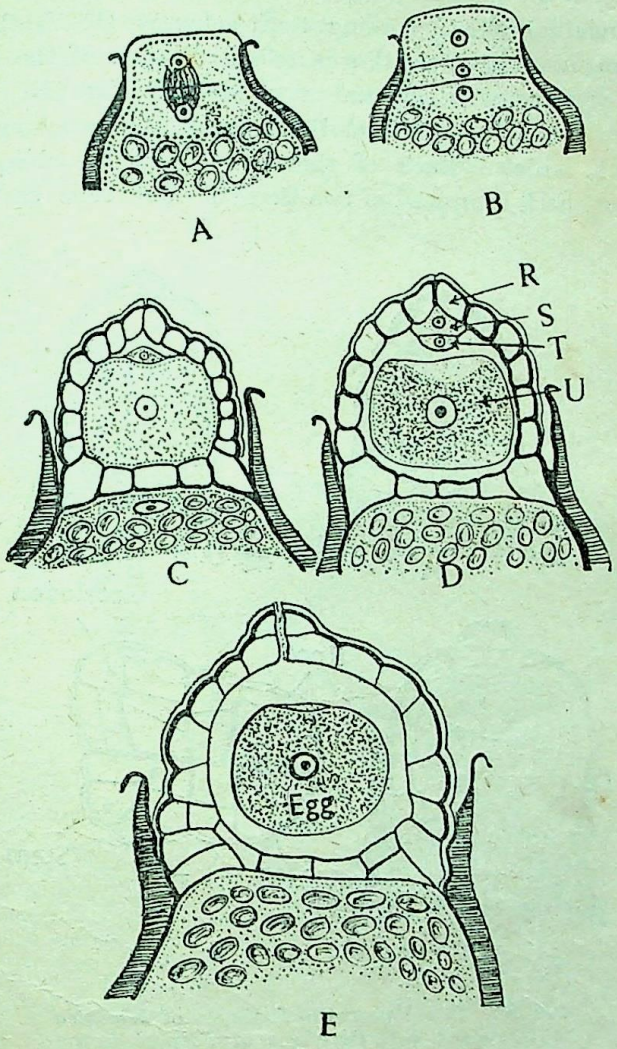

FIG. 81. Development of archegonium. (*A-E*) *A—C* Stages in the development of archegonium ; *D*, Mature archegonium ; *E*, Archegonium awaiting fertilization; *R*, Neck ; *S*, Neck canal cell ; *T*, Venter canal cell ; *U*, Egg)

phyte, although, the megaspores, germinate soon, is slightly slower than that of the male gametophyte and takes 14 to 22 hours.

According to Campbell (1892) the nucleus divides within two to three hours and this is followed by a transverse wall along the line of

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junction between the densely grannular and the watery portions of the cytoplasm The **basal cell** does not divide and serves as a store of food. From the small **apical cell** develops the female gametophyte by repeated divisions The small apical cell has three lateral and one basal cutting faces. These cut off a single segment at each face before functioning as an **archegonial initial.** According to Strasburger (1907) the development of archegonium begins with a periclinal division of the archegonial initial into a **primary cover cell** and **a central cell** (Fig. 81). The former undergoes two successive anticlinal divisions resulting in a four quadrately arranged **neck initials.** Each of these undergoes an oblique division forming a short **neck** composed of two tiers of four cells each. By this

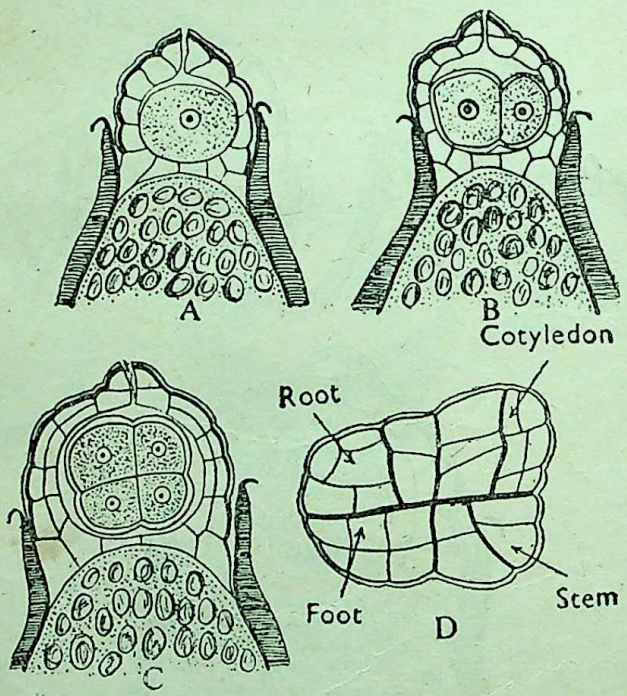

FIG. 82. Development of Embryo of *Marsilea* *A*, Oospore ; *B-C*, Divisions of oospore in the development of embryo ; *D*, Embryo showing differentiation into stem, cotyledon, root and foot.

time, the central cell divides into a small **primary canal cell** and a large globose **venter cell.** The primary venter cell divides to form a small **venter canal cell** and large globose **egg.** The result is a small cluster of cells which form hardly more than a small and simple **archegonium.** The wall of the papilla splits, as the archegonium grows. The mature archegonium with a short neck of two tiers of cells, a neck canal cell, a venter canal cell, and an egg protudes. When mature, the neck canal

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cell and venter canal cell disorganise thus opening the archegonial neck for the entry of sperms. The megaspore at this stage gets surrounded by a gelatinous matrix which is usually thickest in the region of the female gametophyte.

Fertilization. The **chemotactic** sperms are attracted towards the gelatinous envelope and most of them enter, some reaching the archegonium others failing to do so. Only one fuses with the egg and the others become trapped in the gelatinous material nearby. The sperms are greatly stretched out as they die. According to Atkinsin (1943) the orienta-

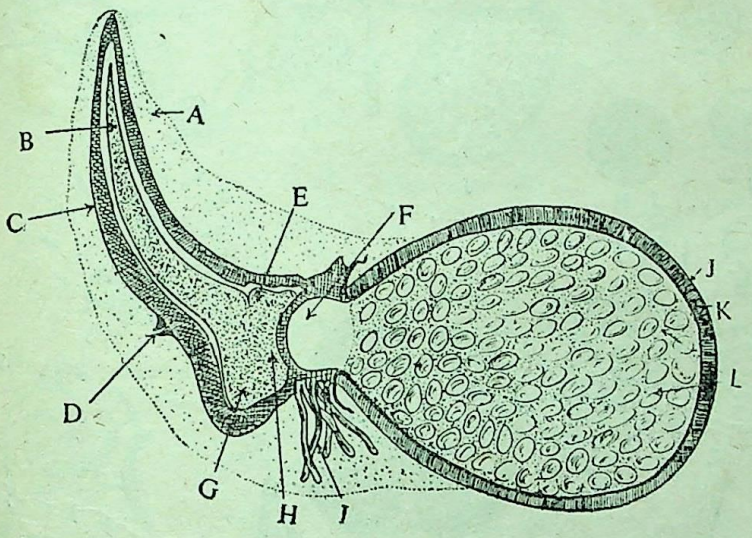

FIG. 83. Median L. s. of a young sporophyte of *Marsilea sp.* still attached to the megaspore; *A*, Mucilagenous envelope; *B*, Primary leaf; *C*, Calyptra-like sheath of the prothallium; *D*, Neck of archegonium; *E*, Stem; *F*, Female gametophyte; *G*, Root; *H*, Foot of embryo; *I*, Rhizoids; *J*. Extine; *K*, Intine; *L*, starch grains.

tion of the sterms becomes reversed (*i. e.* posterior end forward) as it penetrates the egg nucleus. The result of the fertilization is a diploid zygote.

Development of Embryo. The development of embryo takes place rapidly and a sporophyte with the first leaf several mm. long is formed within 2 to 4 days after fertilization. The first division of the zygote is parallel to the long axis of the archegonium *i. e.*, **vertical** (Fig. 82). Later on the two daughter cells of the zygote undergo a division in a plane perpendicular to that of the first division. Thus a **quadrant** embryo is formed. The outer segments of this form **leaf** and **root**, the two inner **stem**

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and **foot.** With the development of embryo, the cells of the venter are

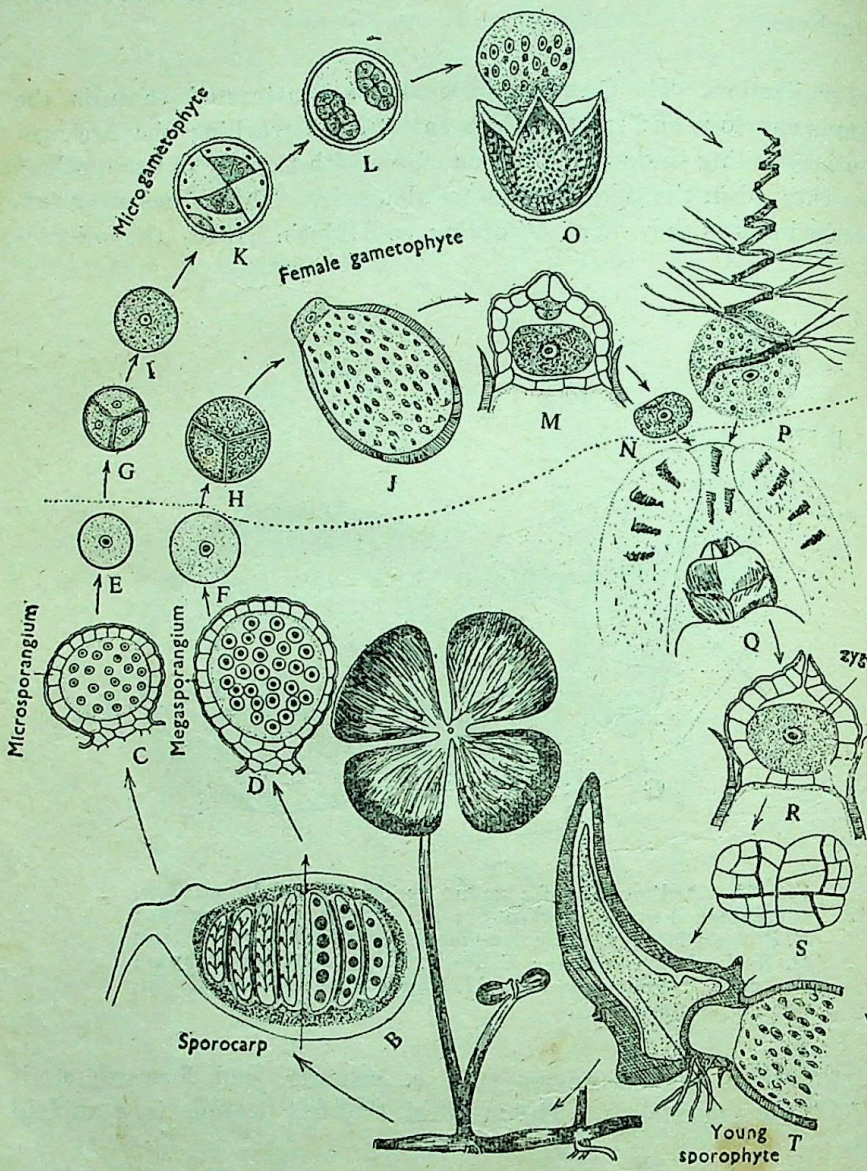

FIG. 84. Diagrammatic representation of the life history of *Marsilea* *A*, sporophytic plant ; *B*, Dorsoventral section of sporocarp showing micro-and megasporangia ; *C*, Microsporangium ; *D*, Megasporangium; *E*, Microspore mother cell (2x); *F*, Megaspore mother cell (2x) ; *G*, Tetrad of microspores ; *H*, Tetrad of megaspores ; *I*, Microspore. (x), *J*. Megaspore (x) ; *K*, *L*, *O*, Development of male gametophyte; *M*, Archegonium , *N*. Egg ; *P*. Sperm ; *Q*. Megaspore showing fertilization of archegonia with sperms in mucilagenous cone ; *R*, Oospore ; *S*, Embryos ; *T*, Young sporophyte.

stimulated to divide periclinally and form a growing sheath—the *calyptra*

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which surrounds the young sporophyte (Fig. 83). A few of the rhizoids develop from some of the lowest cells and the upper tissues become green. Growth of the calyptra keeps pace with that of the embryo for the first four or five days but this disappears about the some time when the primary root penetrates the soil or substratum. The embryonic sporophyte grows rapidly. According to Bold, "one series of germ ling

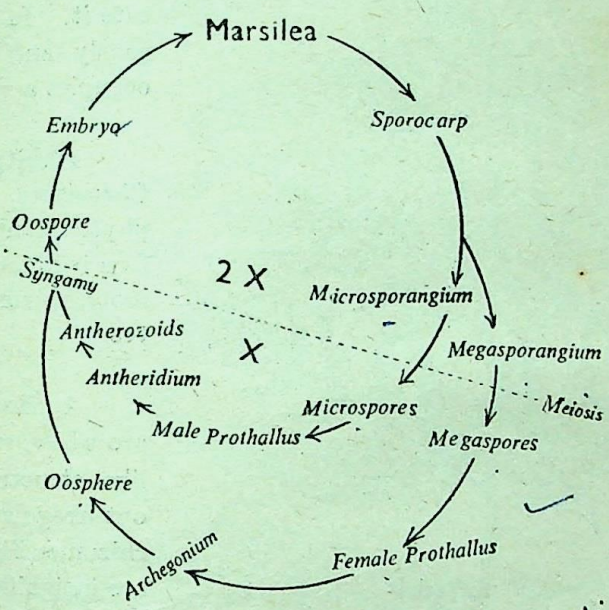

FIG. 85. Life cycle of *Marsilea*

sporophytes of *M. vestita* planted in April produced mature plants bearing sporocarps by the following October."

PTERIDIUM ("The Braken Fern")

Systematic position :

Division—*Tracheophyta*

Sub-division—*Pteropsida*

Class—*Filicales*

Order—*Leptosporangiate*

Family—*Polypodiaceae*

Genus—*Pteridium*

Occurrence. Like all other ferns it is also found in moist and shady places. However, it prefers open places and needs little shade. On

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account of this special habit it is also called "Sun fern". It grows on hills in the temperate climate. It also grows in cultivated fields and once it comes out, it is very difficult, though not impossible, to eradicate it. It grows vigorously and very soon occupies a vast area.

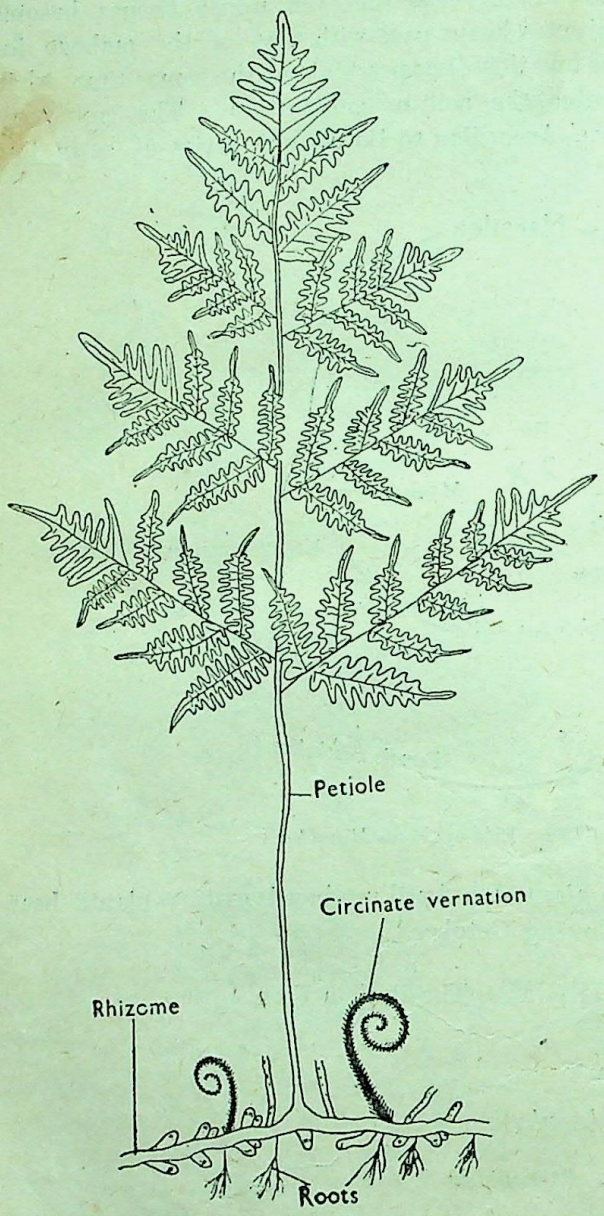

Fig. 86 Habit of *Pteridium*.

Habit and External Characters. The sporophytic plant body of the fern is differentiated by roots, rhizome and leaves.

1. **Roots.** They are white, small, thread-like structures coming out irregularly from the rhizome (Fig. 86). They are insignificant in their function. In a cross section they exhibit a diarch structure.

2. **Rhizome.** The underground stem or the rhizome is a long, slender dichotomously-branched structure which runs horizontal to the ground. It has nodes and internodes. It is brownish or black in colour and soon spreads in various directions giving rise to adventitous roots below and leaves above (Fig. 86).

In a cross section the rhizome does not appear completely circular. It is a polystelic structure but in its gross anatomy it differs from other ferns (Fig. 87 A.) A. T. s. of the rhizome under the microscope exhibits the following structures.

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(a) **Epidermis.** The outermost single, layered sheath is of epidermis. It may be thick (Fig. 87 B)

(b) **Sclerenchymatous hypodermis.** Just beneath the epidermis there is the multilayered sclerenchyma. It is not continuous but is

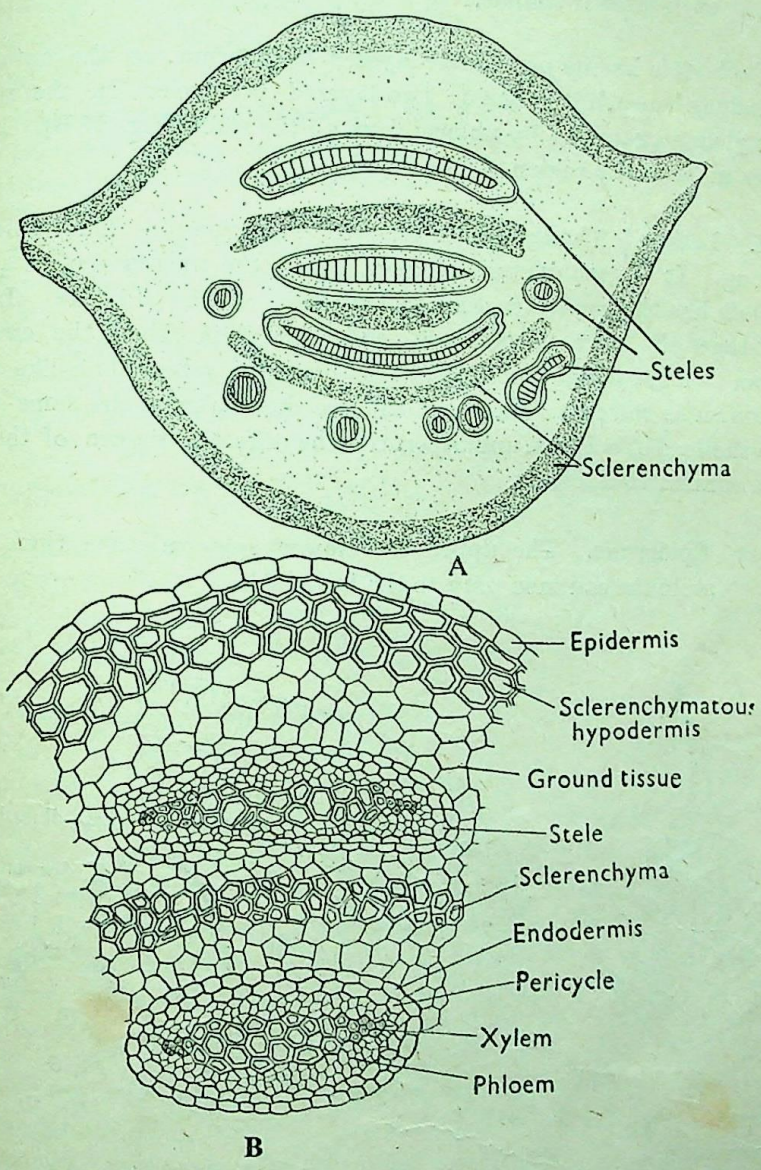

FIG. 87. T. s. of the rhizome of *Pteridium*, *A*, Polystelic structure. Steles lying in the ground tissue ; *B*, Gross anatomy showing all the tissues in details.

broken at two points as shown in (Fig. 87. A). At these two points it is replaced by ordinary parenchyma.

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(c) **Ground Tissue.** It is made up of the parenchymatous cells and it is in this tissue that the many steles lie embedded.

(d) **Vascular Strand.** It comprises of many steles which are of different shape and size. Generally the steles and the sclerenchyma alternate with each other (Fig. 87 A). The structure of each stele is similar.

Each stele has its own single-layered endodermis as the outermost layer. Just beneath it is one or two-layered pericycle. In the middle is the xylem surrounded by phloem from all the sides (Fig. 87 B). Xylem occupies most of the region of the stele.

3. **Leaves.** The leaves are pinnately compound. The petiole is quite long. It has many steles if seen under the microscope in a t. s. Each stele has the same structure as the stele of the rhizome. In the young stages the leaves are (Fig. 86) coiled and it is called the **circinate vernation** The young leaf possesses brownish silken hair-like structures known as **ramenta.** In a c. s. the leaf shows almost the same structure as the leaf of a dicot. angiosperm. The different tissues of the leaf may be summarized below.

(a) **Epidermis.** The upper and lower epidermis are there with stomata confined only to the lower side.

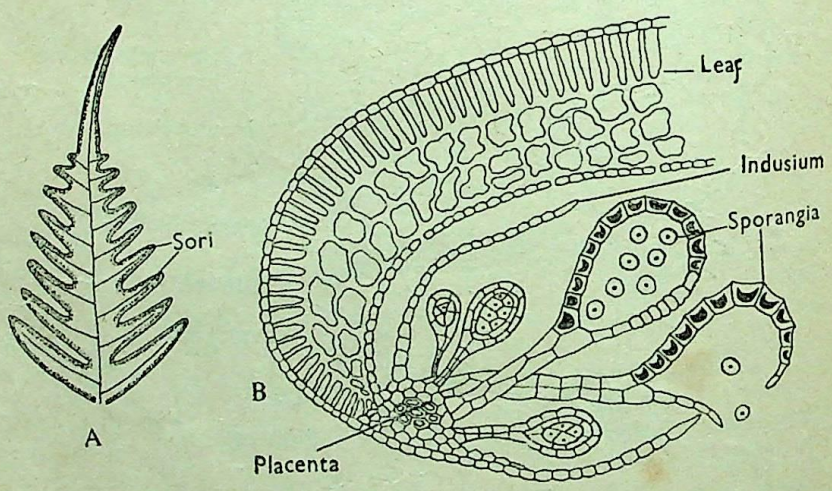

FIG. 88. *A*, Sporophyll with marginal sori ; *B*, Section of the leaf passing through a sorus showing placenta, indusia and many sporangia of different stages.

(b) **Palisade.** One to three-layered palisade with vertically arranged cells lies just beneath the upper epidermis.

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(c) **Spongy tissue.** Most of the region of the leaf is occupied by the spongy parenchyma the cells of which are loosely arranged (Fig. 88. B).

Reproduction. It is brought about by two methods :

1. *Vegetative*
2. *Sexual*

1. **Vegetative Reproduction.** By death and decay of the older parts of the rhizome reaching dichotomy. The bifurcated portions separate and act as two individuals.

A new sporophyte comes out from the portion of a leaf, if the latter touches the soil and remains buried in it.

2. **Sexual Reproduction.** The fern leaves when mature develop sori and are called **sporophylls.** The sori are marginal in development. They appear as black or brown streaks running all along the leaf margin (Fig. 88 *B.*). In a section of the leaf passing through the sorus, the following structures can be seen.

The margin of the sporophyll is slightly swollen which constitutes the placenta. Many sporangia are borne on it. The sporangia remain protected by two flaps of indusia (Fig. 88. B.). Indusium is one-celled thick. Each sporangium possesses a stalk and a capsule.

Development of the Sporangium. It is leptosporangiate in development. The sporangium initial arises from a single superficial cell of the placenta. The initial soon protudes out slightly and divides into two—an inner cell (which may further divide or not) and an outer cell. The latter divides by three diagonal walls in such a way that a three-sided pyramidal cell is formed (Fig. 89. A, B). This pyramidal cell cuts off 4—5 segments from its three lateral cutting faces. The segments undergo many more divisions and form the wall of the capsule which remains one cell thick. The lateral segments cut off cells below which form the stalk of the sporangium (Fig. 89. C, D).

In the meantime the pyramidal cell divides into two—an inner pyramidal cell or the archesporium and an outer jacket initial (Fig. 89 D). The inner pyramidal cell cuts off cells from each of its four faces which undergo anticlinal and periclinal divisions and ultimately give rise to tapetum. The tapetal layer is two-celled thick (Fig. 89 E, F) and it supplies food to the developing spores The cell now left out in the centre after the formation of the tapetum (Fig 89, E, F) is the sporogenous cell. It divides and gives rise to spore mother cells.

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Each spore mother is a diploid structure but sooner or later it divides meiotically and forms four haploid spores. According to Bower (1899)

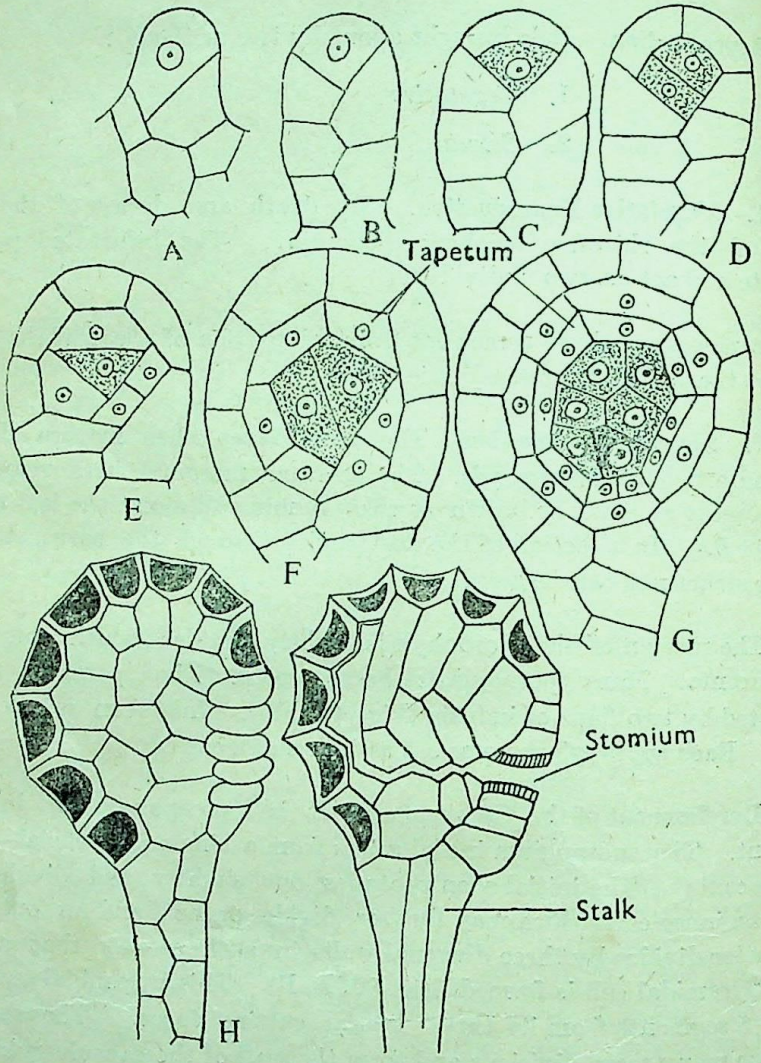

FIG. 89. Development of sporangium. A—*C*, Development of pyramidal cell and stalk of the sporangium. *D*—*F*, Sporogenous cell, tapetum and wall of the sporangium ; *G*, Spore mother cells in a sporangium ; *H*, Sporangium showing the formation of stonium; 1. Dehiscence of the capsule.

the latter may not be sixty-four completely, as some of them always degenerate. The jacket initials divide and form annulus which covers three-fourth of the sporangium. It is highly cuticularized and is dark in colour (Fig. 89, H).

Dehiscence of the Capsule. It is the annulus which brings about the dehiscence of the capsule. When the water evaporates from the cells of

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annulus, the outer walls of the cells are taken inwards. By the inward movement the walls become concave. Now greater the loss of water, more is the concavity. This ultimately brings about the required dehiscence. The ruptured portion is the stomium which forms the mouth of the capsule (Fig. 89, I) from where spores escape to the outside So the spores are liberated in dry conditions.

Germination of the spores and formation of prothallus. The spores after being shed from the capsule remain viable for sometime. When a spore reaches a suitable place it germinates sending out a small tube (3—6 celled) in the beginning. This tubular structure ultimately becomes heart-shaped and is called the prothallus. It has an apical notch and in the earlier stages it is one cell thick (Fig. 90). Later on it becomes more

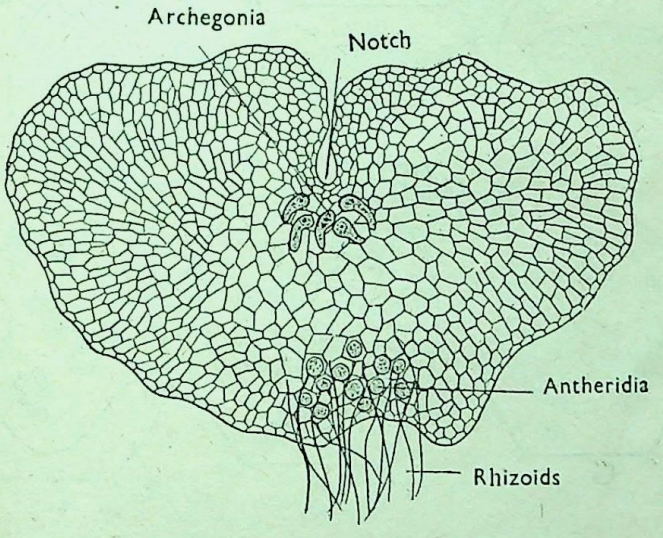

FIG. 90. Mature prothallus of *Pteridium* as seen from below.

than one cell thick in the posterior region where rhizoids also develop. It is on this prothallus that the male and female organs of reproduction are developed. Antheridia, the male organs of reproduction develop earlier than the archegonia, the female organs of reproduction.

Development of an Antheridium. The ordinary vegetable cell of the heart shaped prothallus gives rise to the antheridium initial which directly acts as antheridium cell (Fig. 91 A) The latter divides by a transverse wall into two—an upper cell and an inner first ring cell R' (Fig. 91 B). According to Davie (1951) the turgor in the upper cell is greater than the turgor in the lower cell with the result that the already laid transverse wall stretches more towards the base of the lower cell (Fig. 91 C). Now the upper cell divides

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again by a transverse wall into a dome cell and a primary androgonial cell (Fig. 91, D). The dome cell further divides into a cover cell and a second ring cell R^2 ((Fig. 91, E). The two ring cells R^1 and R^2 so formed together with the cover cell form the jacket of the antheridium

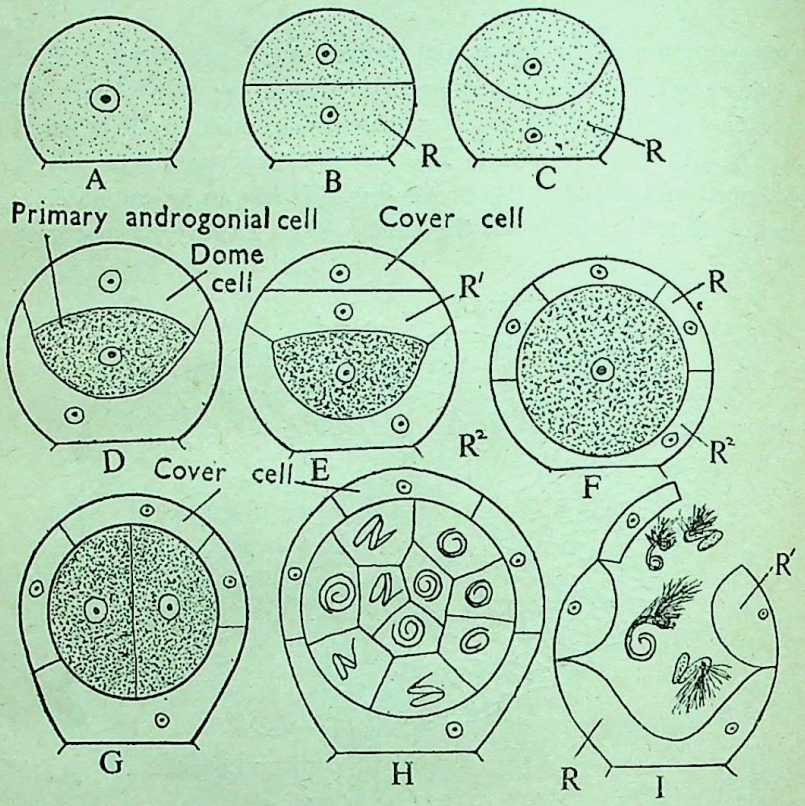

FIG. 91. Development of antheridium of *Pteridium*. *A*, Antheridium initial; *B*, First ring cell; *C*, Stretching of the transverse wall towards the base ; *D—E*, Formation of dome cell, cover cell, and second ring cell; *F*, Antheridium with outer jacket; *G—I*. Formation and liberation of antherozoids.

(Fig. 91 F). The primary androgonial cell divides repeatedly and gives rise to many androgonial cells. The last generation of these cells is called the androcytes. The latter may be 30—40 in an antheridium and ultimately they metamorphise into antherozoids (Fig. 91, G—I). Each antherozoid is uninucleate and multiciliate.

The antheridia absorb water and ring cells swell. This creates a pressure inside. Finally the cover cells open out liberating all the antherozoids which go wriggling through the water for sometime until they reach near an archegonium

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Development of an Archegonium. The developmont of the archegoninm is very simple. The archegonium initial develops near the notch (Fig. 92, A) and soon divides by two transverse walls into three cells (Fig. 92 B)—a basal cell which does not take part further in the

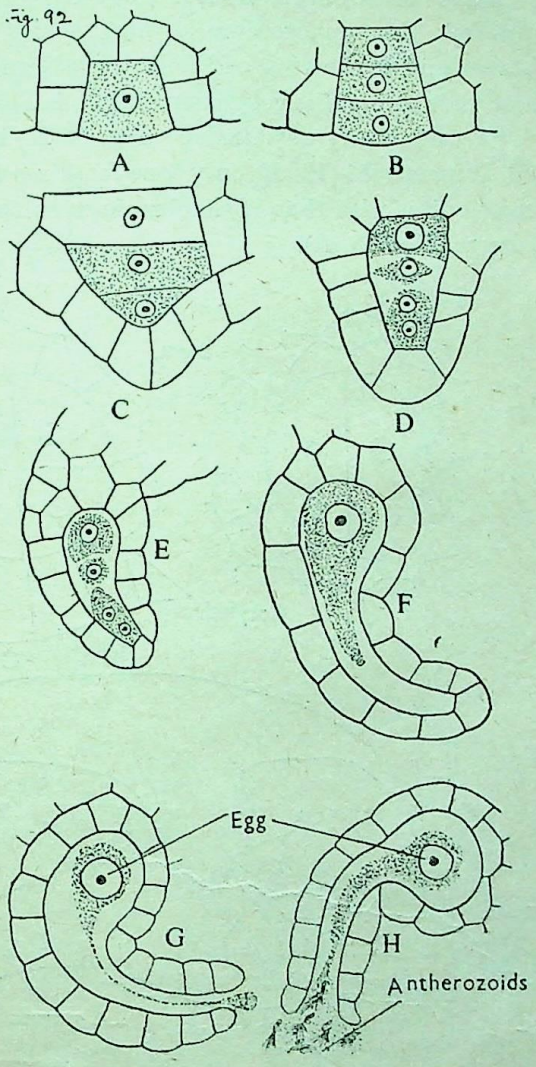

FIG. 92. Development of Archegonium in *Pteridium*. *A*, Archegonium initials ; *B*, Formation of three cell ; *C—E*. Formation of neck and venter ; *F*, Mature archegonium ; *G*, *H*, Fertilitation.

development of the archegonium, a central cell and a primary cover cell. The latter divides vertically and forms four neck initials which later on divide transversely and give rise to a neck of 3-7 cells in height (Fig. 92, forms D-F). The central cell and the

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most prominent egg (Fig. 92 E). The archegonia are sharply curved towards the posterior end of the prothallus.

Fertilization. Each archegonium, at maturity, opens out and its primary canal cell and ventral canal cell disorganize (Fig. 92. F). It sends out a gelatinous mass from its neck (Fig. 92 G). The antherozoids are attracted towards the archegonium owing to the presence of this gelatinous substance and so the view of Pfeffer (1884) and Shibata (1911) that the antherozoids are positively chemotactic is absolutely correct. Many antherozoids find their way inside (Fig. 92 H) but according to Shaw (1898) and Yamanouchi (1908) only one fertilizes the ovum. The nucleus of the male unites with that of the female resulting in the formation of an oospore (Fig. 93, A).

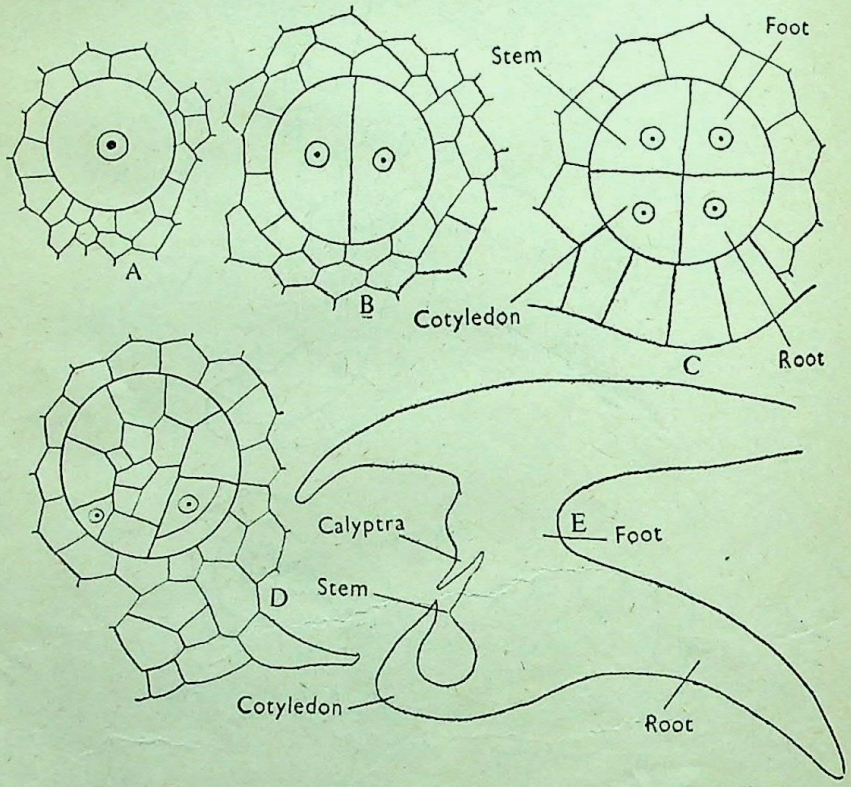

FIG. 93. Post-fertilization stages in *Pteridium*. *A-B*; First and second divisions in oospore. *C—E*, Further divisions and formation of new sporophyte.

Post Fertilization stages and Formation of a New Plant. Just after fertilization the diploid ovum increases in size and divides into two by a vertical wall (Fig. 93 B). Thus two cells are formed—an epibasal cell towards the apex of the prothallus and a hypobasal cell facing the

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base. A wall is again laid down at right-angles to the first and thus a

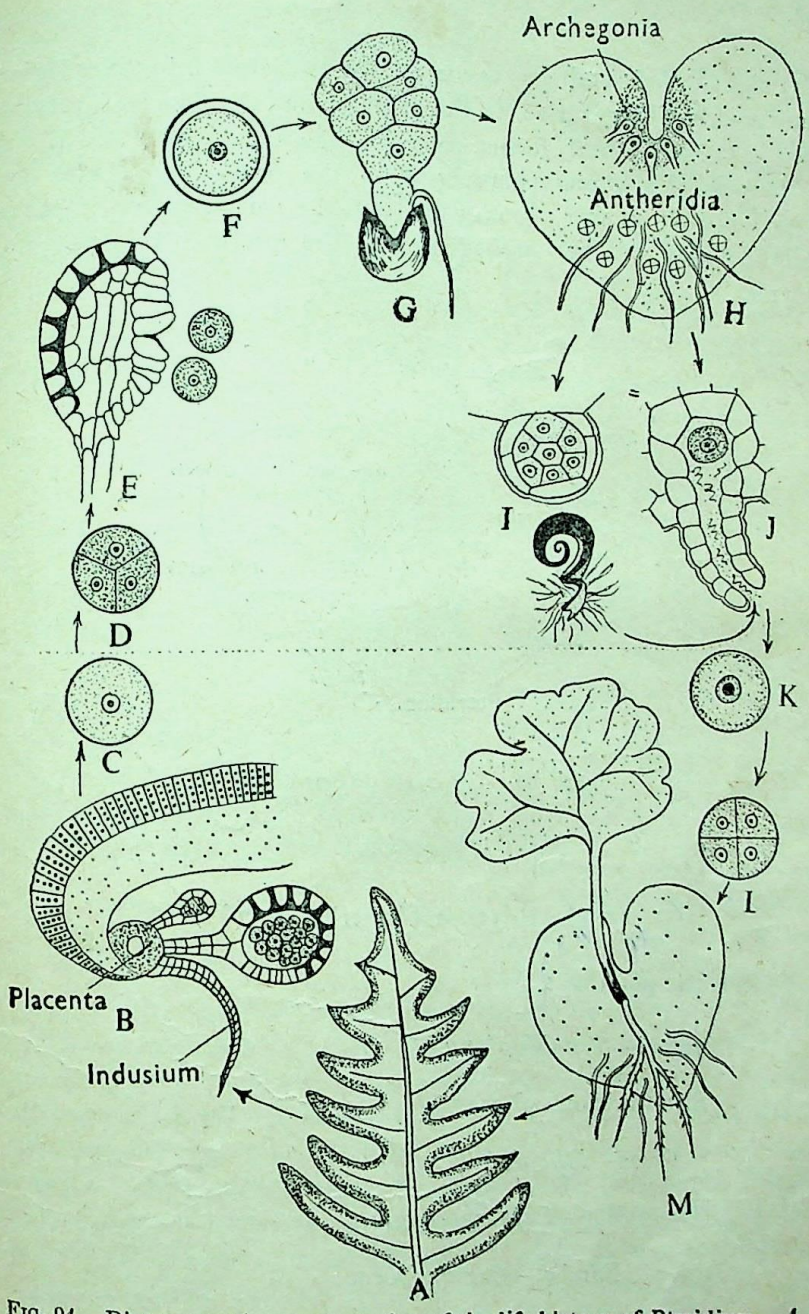

FIG. 94. Diagrammatic representation of the life history of *Pteridium*. *A*, sporophyll from a sporophytic plant; *B*, T. s. of sporophyll showing sporangia, indusium and placenta; *C*, Spore mother cell (2x); *D*. Tetrad of spores (x); *E*, Mature sporangium showing dehiscence of spores through the stomium; *F*, A spore; *G*, A germinating spore developing prothallus; *H*; Mature prothallus showing antheridia and archegonia on the ventral side; *I*, An antheridium and sperm; *J*, A mature archegonium having a number of sperms in the neck; *K*, Zygote; *L*, Development of embryo; *M*, Young sporophyte from the prothallus.

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quadrant is formed. By a further division, the quadrant becomes an octant.

The eight-celled embryo becomes differentiated into different parts. The epibasal half gives rise to the stem tip and the first leaf (cotyledon) and the hypobasal half forms root and the foot (Fig. 93. C—E). The latter fastens the young sporophyte to the prothallus. Later on the embryo increases in size accompanied by the enlargement of the surrounding tissue of the archegonium. The prothallus persists for a long time.

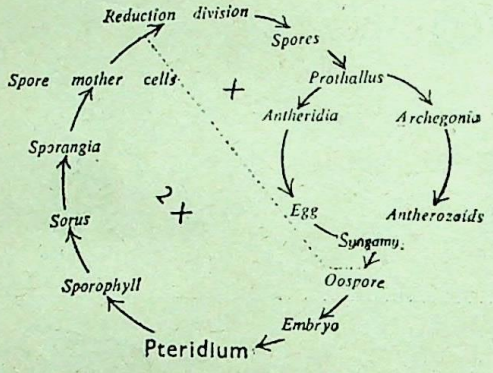

FIG. 95. Life cycle of *Petridium*.

OSMUNDA

("The Royal or Flowering Fern")

Systematic position :

Division—*Tracheophyta*

Sub-division—*Pteropsida*

Class—*Filicales*

Order—*Leptosporangiate*

Family—*Osmundaceae*

Genus—*Osmunda*.

Distribution and Occurrence. Osmunda (*Osmunder*, Saxon, equivalent to God Thor) is an important genus, on account of certain peculiarities which are regarded as intermediate between the eusporangiate and leptosporangiate ferns. The genus is cosmopoliton in distribution and

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has been found in fossilized form from the Jurrasic. It is usually found in boggy places especially in moist regions of the West and North. *Osmunda* is very well represented by 12-14 species out of which three are very common in India.

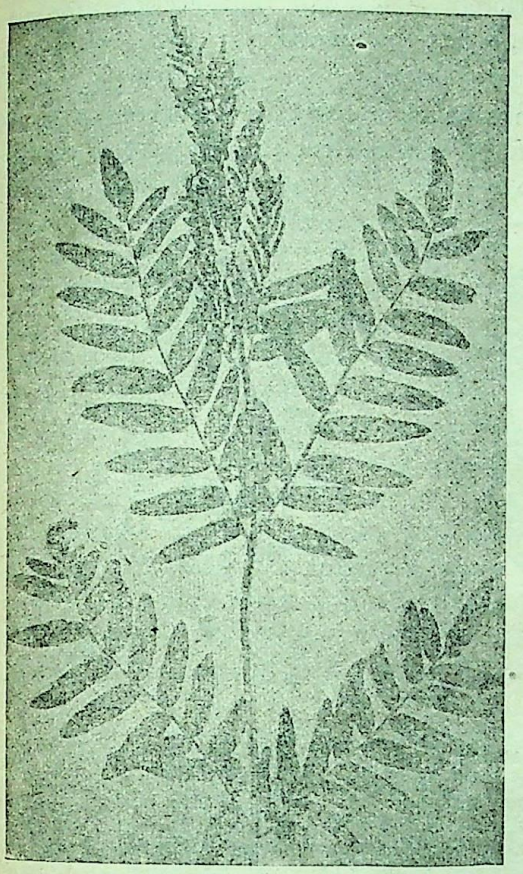

Fig. 96. Habit of *Osmunda regalis*. Note the fertile frond showing upper sporangiferous pinnae and the lower vegetative ones.

Osmunda regalis "the Royal" or "Flowering fern" is found in South India and Himalayas ; *O. clatoniana* the "interrupted fern" found in Mysore and Himalayas ; and *O. cinnamomea*, the "cinnamon fern". The plants are ornamental.

Habit and External Characters. The plants are perennial with subterranean stems and a crown of large magnificent leaves which attain a length of 6 feet (Fig. 96). The leaves are uni-or bi-pinnately compound depending upon the species. The leaflets or pinnules are arranged more or less regularly in opposite pairs on the long rachis. The pinnately compound leaves are known as fronds. Each pinnule is attached by a short stalk and has a single mid-rib. The pinnae are leathery in texture and show open dichotomous venation. The underground stem or rhizome is called the **"stock"**. From this arise a group of circinately coiled fronds which unfold and after photosynthesizing produce spores. The leaves are **annual** in that they last only for one season but their sclerenchymatous bases persist forming a prominent armour around the vertical rhizome. Some species have **dimorphic** leaves *i.e.*, fertile and sterile. In such cases the fertile leaves appear before the sterile ones when a new set of leaves is unfolded. A few species have all leaves fertile and the production of sporangia restricted to the pinnae at the middle or at the apex of the blade as in *O. clatoniana*. The stem has numerous adventitious wiry roots, two of which arise at each leafbase.

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Anatomical Structure All the vegetative organs *i.e.*, the stem, the leafbases and the roots are so closely associated, that sections for all are usually available for study in a single preparation.

Stem. According to Gwynne-Vaughan (1911) a transverse section of a very young stem show a **protostelic** structure but gradually as it

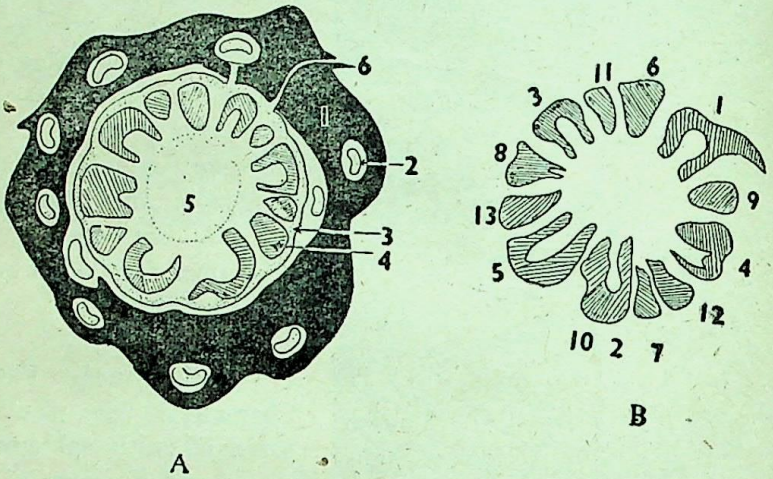

FIG. 97.–A. T. s. of a strong stem of *O. regalis* Note the vascular tissue is broken up into a number of 'u'-shaped separate stands separated by narrow parenchymatous leaf gaps ; *1*, Outer thick rind with leaf traces ; *2*, Leaf traces ; *3*, Phloem ; *4*, Xylem ; *5*, Pith ; *6*, Lowest leaftrace bundle with a root bundle going off from it through the rind. FIG. 97.–B. Diagrammatic sketch of vascular bundle cylinder of Fig. 97–A highly magnified. *1*. The lowest leaftrace bundle cut through exactly where it enters the cylinder with one of the two root bundles which are attached to it at this point ; *1–13*, the leaftrace-bundles of the thirteen successive leaves seen in the T. s. (10 being united abnormally with 2.)

matures pith begins to develop in the centre so that the stem becomes **siphonostelic.** The ring of vascular tissue is finally broken into a number of **'u'-shaped** separate strands separated by narrow parenchymatous **leaf-gaps** (Fig. 97). The arrangement is not truly dictyostelic, as some authors believe (Fig. 98), because there is a common endodermis surrounding the entire ring of vascular strands. These are, therefore, only portions of the broken vascular cylinder which have often been regarded as meristeles by some workers. The structure of the mature stem of *Osmunda* is peculiar in that it shows superficial resemblance to the ring of vascular bundles in a dicotyledonous stem, but the Osmunda stem possesses a continuous ring of **phloem** (Fig. 97 A) which is many-layered between the xylem strands and is comparatively thin opposite them. A further peculiarity is that the **endodermis** does not open at the

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passage of the leaftrace from the stele to the cortex. This is brought about by the union of the endodermis which surrounds the leaftraces with that which surrounds the stele, at the point of contact between the two, so that at no place, except occasionally at the base of a branch, is there any uninterrupted continuity between the medulla and the cortex. The **xylem** strands are **mesarch** in that the protoxylem is surrounded by metaxylem and lies towards, the outside of the xylem groups (Fig. 99). The metaxylem are composed largely of scalariform-pitted tracheids and have been shown to be in open connection with one another and hence regarded as vessels by Mcleans and Ivimey Cook. The **phloem** deserves mention because its sieve tubes reveal callus strands near the sieve-plate which are covered by minute slimy globules of uncertain nature. The phloem is surrounded by 2-4 layers of

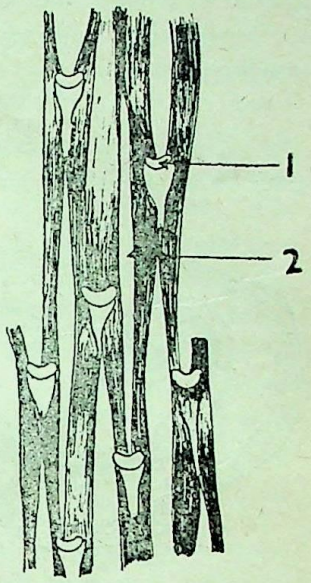

FIG. 98. Portion of stele of *O. regalis* dissected to show dictyostelie structure (*1*, Leaftrace ; *2*. Leafgap)

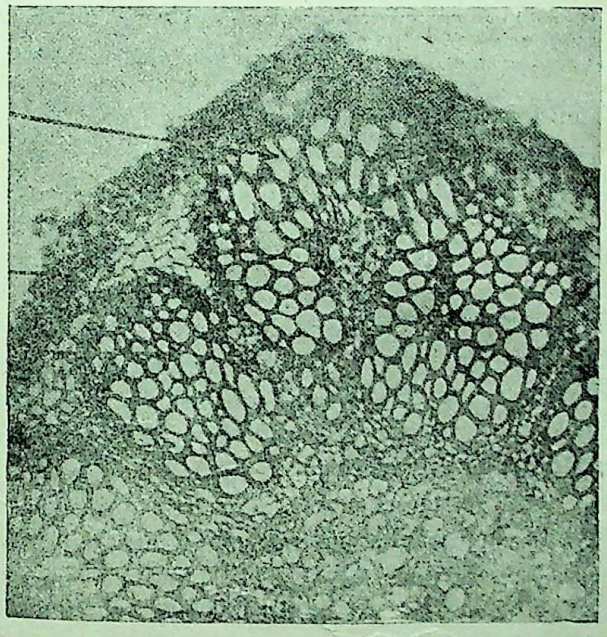

FIG. 99. Photomicrograph of vascular tissues of stele showing mesarch protoxylems (*1*, Leaftrace ; *2*, Phloem ; *3*, Protoxylem ; *4*, Metaxylem ; *5*, Pith.

thin-walled parenchymatous pericycle which in turn is surrounded

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by a suberized endodermis. Usually there is only one **endodermis** as seen in *O. regalis*, but sometimes an inner incomplete endodermis makes its appearance and separates the stele from the central pith *e.g.*, *O. cinnamomea.*

The cortex consists of inner parenchymatous colourless region and a dark staining outer sclerenchymatous region. Both portions of the cortex contain spirally arranged **c-shaped** leaftraces, each surrounded by an endodermal layer and occupy a very large area of the entire section of the stem, whereas the actual stem tissue occupies 1/7 of it.

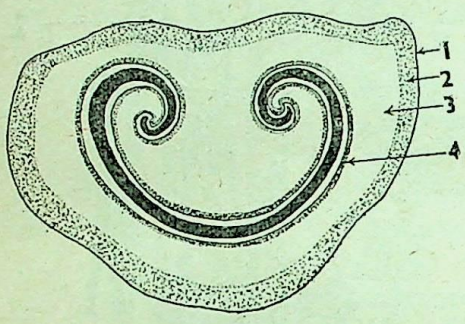

FIG. 100. Diagrammatic T. s. of petiole of *O. regalis*. (1) Epidermis ; (2) Sclerenchymatous hypodermis ; (3) Parenchymatus ground tissue ; (4) C-shaped vascular strand. Xylem shown by solid black colour. Phloem is represented by blank space in the vascular strand.

Petiole. The petiole reveals a more or less triangular outline with a characterstic c-shaped vascular strand (Fig 100). Each leaf-base contains a petiolar stele which is surrounded by dark brown band of sclerenchyma. This in turn is covered by a broad parenchymatous **cortex**. These soft parenchymatous cells are so closely packed together around the stem that they may easily be mistaken for an extension of the cortex of the stem. "The **stele** in each petiolar trace passes downwards and inwards through the true cortex of the stem and enters the stele as a horse-shoe shaped mass of xylem and phloem. The **xylem** possesses one protoxylem on its inner concave side which passes into the ring and takes its place there at the base of a gap." The curved outline of the leaftrace bundle is due to the fusion of two stelar bundles below the point of junction of stele and leaftrace to form one leaftrace The xylem is formed of scalariform tracheids and is surrounded by a zone of phloem and a single-layered endodermis. This is surrounded by cortex which is differentiated into three regions : the **outer** and **inner** parenchymatous regions and the **middle** sclerenchymatous The sclerenchyma of separate petioles fuses into a solid mass, close to the actual stem, and contributes to great rigidity of the stem.

The petiole of an osmunda leaf differs from those of most other leptosporangiatae in the **stipule** like expansion at its base. The vascular bundle of the petiole is similar in shape to the leaftrace, but is without a conspicuous endodermis.

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Leaflet. A transverse section of the lamina reveals an outer **epidermis**, below which lies a **mesophyll** composed of irregular parenchymatous cells with large intercellular spaces. The palisade tissue is conspicuous by its absence, though the mesophyll is denser towards the upper side and more loosely arranged on the lower side. The epidermis and mesophyll cells are chlorenchymatous in nature. Below the mesophyll lies the **lower epidermis** which is punctured here and there due to the presence of stomata. There is a single **mid-rib** on either side of which are pinnate veins.

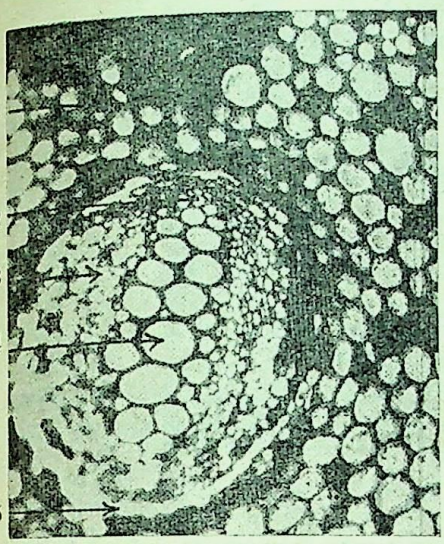

FIG. 101. Photomicrograph of a part of the diarch root of *O. regalis* (T. s) *1*, Cortex; *2*, Protoxylem; *3*, Phloem; *4*, Metoxylem; *5*, Endodermis.

Root. A pair of roots arise endogenously near each leaf base. A transverse section reveals a broad **cortex** and an exarch **protostele** (Fig. 101). The roots are **di**— or **triarch** in structure. The radial vascular bundles of xylem and phloem are surrounded by two layers of **pericycle** and an **endodermis**. The cells of the cortex bordering the endodermis are thin-walled, whereas those towards the outside are thick-walled.

Vegetative Propagation. Lang observed very much reduced leaves in starved plants which appear as short cylindrical outgrowths without a lamina. The apices of these may be directly transformed into abnormal growth buds. These buds are capable of developing normal leaves in regular succession. According to Wardlaw the actual transformation of leaf into a shoot takes place by shifting of a broad apex, laterally to a leaf rudiment.

Reproduction. The initiation of reproduction is associated with the modification of leaf structure which develop **sporanagia** (Fig 102). The location of the sporangia varies with the species. In *O. regalis* they develop on the most **distal pinnae**; in *O. clatoniana* **certain intermediate pairs of pinnae** bear sporangia, the distal pinnae are sterile; whereas in *O. cinnamomea* the sporangia are borne only upon **special sporophylls** (Fig. 103). According to Bower 1889 these arise super-

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ficially as small convex protuberances on the surface of the pinnu-

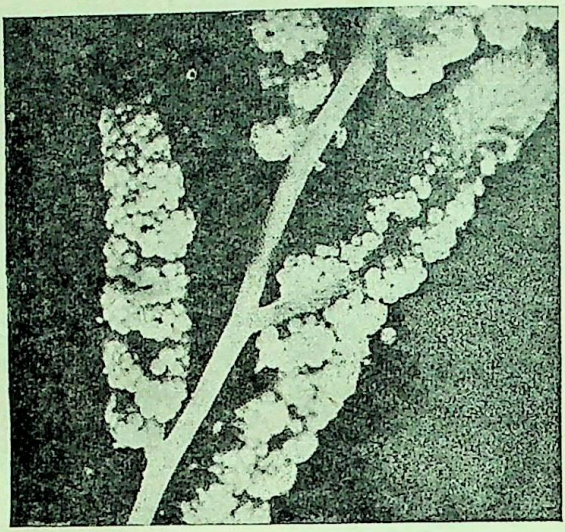

FIG. 102. Enlargement of fertile tip of frond. Note transition between blade-like and nonblade-like segments.

les. Though there is a single prominent sporangial initial cell, but

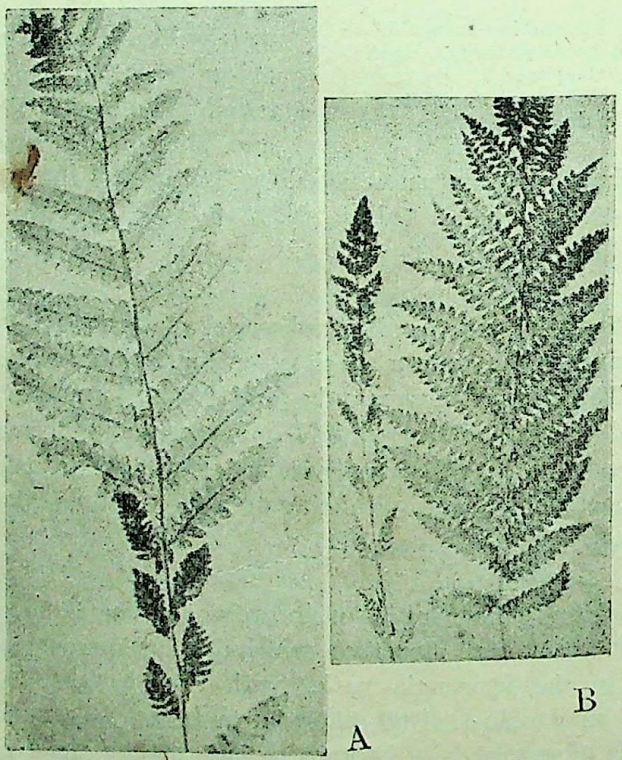

FIG. 103. Variation in the location of sporangia *A, O. claytoniana* showing fertile pinnae among vegetative ones; *B, O. cinnamomea* the sporangia are borne on special sporophylls shown at the left, vegetative frond is shown at the right.

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several adjacent cells also contribute to the sporangium formation in general and to its thick stalk in particular. This is an abnormal feature for leptosporangiatae.

The **sporangial initial**, whether cubical or pyramid in form divides pereclinally into an outer **jacket initial** (primary wall cell) and an **inner archesporial cell** (Fig. 104). The jacket initial divides anticlinally to form a single layer of jacket cells forming the **wall** of the sporangium. The archesporial cell cuts off a flat cell from each of its faces thus functioning as an internal apical cell. The result of this is the formation of a perepheral layer of cells forming the **tapetum.** After the production of this tapetal layer the archesporial cell functions as the **primary sporogenous cell** and undergoes repeated divisions until about 128 sporogenous cells are produced. These behave as **spore mother cells** and divide meiotically to produce between 256 and 512 **spores** in tetrads. The haploid number of chromosomes is 22. During meiosis the tapetal cells

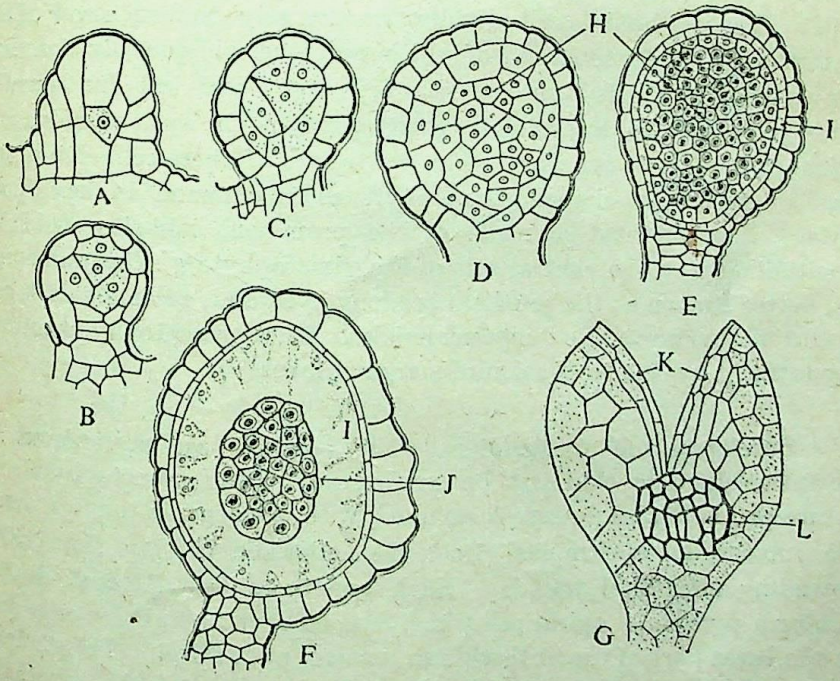

FIG. 104. Development of sporangiam of *O. regalis*. *A*. Initial stages showing cubical or pyramidal sporanigal initial; *B—C*, Pereclinal divisions forming anonte jacket and inner archesperial cells (H); *D—E*, Later stage showing the formation of a perepheral tapetum (I); *F*, Sporangium showing spore mother cells (J); *G*, A ruptured sporangium showing a cap of thickened cells (L) and stomium (K).

elongate greatly, their walls disorganize forming a **plasmodium** which pushes between the dividing spore mother cells. When the sporangium

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matures, a unilateral group of thick-walled cells develops at one side of sthe porangium. This is called **annulus**. A band of elongated thin walled narrow cells—the **stomium**, develops at right angles to the annulus and extends over the sporangial apex down to the stalk. This marks the vertical lire along which the spherical sporangium dehisces.

The spores of *Osmunda*, like those of *Equisetum*, are **green** in colour and show a triradiate ridge which is formed by the compression of the spores into tetrads during sporogenesis. Their chlorophyllous nature does not allow them to remain viable for a long period. They germinate rapidly, under moist conditions, without undergoing any period of rest.

Germination of Spore. On the absorption of water, the outer wall of the spore (exine) breaks along the triradiate ridge so that the inner contents, still enclosed by two inner wall layers, protrude out into a cylindrical cell. This divides transversely, at right angles to the long axis, into a small **rhizoidal cell** and the large **prothallial cell** (Camphell 1892). The prothallial cell divides transversely to form a row of three or four cells, the terminal cell of which undergoes oblique divisions forming an **apical cell**. This cuts off new cells right and left for sometime. This gives rise to a **spatulate gametophyte** at the apex of which many apical cells begin to function. The derivatives of these cells build up a massive green heart-shaped gametophyte as is common in leptosporangiatae. Mention must be made of the prominent **mid-ribs** which runs longitudinally on the ventral side of the gametophyte. The gametophytes, better known as the prothalli are long lived and resemble dark green thallus of liverworts like Jungermanniales. These gametophytes multiply vegetatively by the separation of marginal lobes.

Development of Antheridium. The prothalli are **protandrous** *i. e.*, the antheridium develop first on margins of young gametophyte. The mature prothalli also possess them along with archegonia on its ventral side. According to Camphell (1892) the **antheridia** develop from certain protruding **antheridial initials**. Each undergoes two diagonal divisions forming a pyramidal apical cell which cuts off several tubular cells forming the basal part of the antheridium, known as **pedicel**. This helps in raising the antheridium much above the surface of the prothallus. The pyramidal apical cell divides periclinally by a curved wall cutting off **jacket initial** and a **primary androgonial cell**. The jacket initial divides anticlinally and then obliquely thus forming a single-layered thick **wall** with a triangular **opercular cell** at the top. This resembles the operculum of the eusporangiatae. The androgonial initial

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undergoes successive divisions to form about 100 **androcytes**. Each gives rise to a single, coiled, may cilliated **antherozoid**.

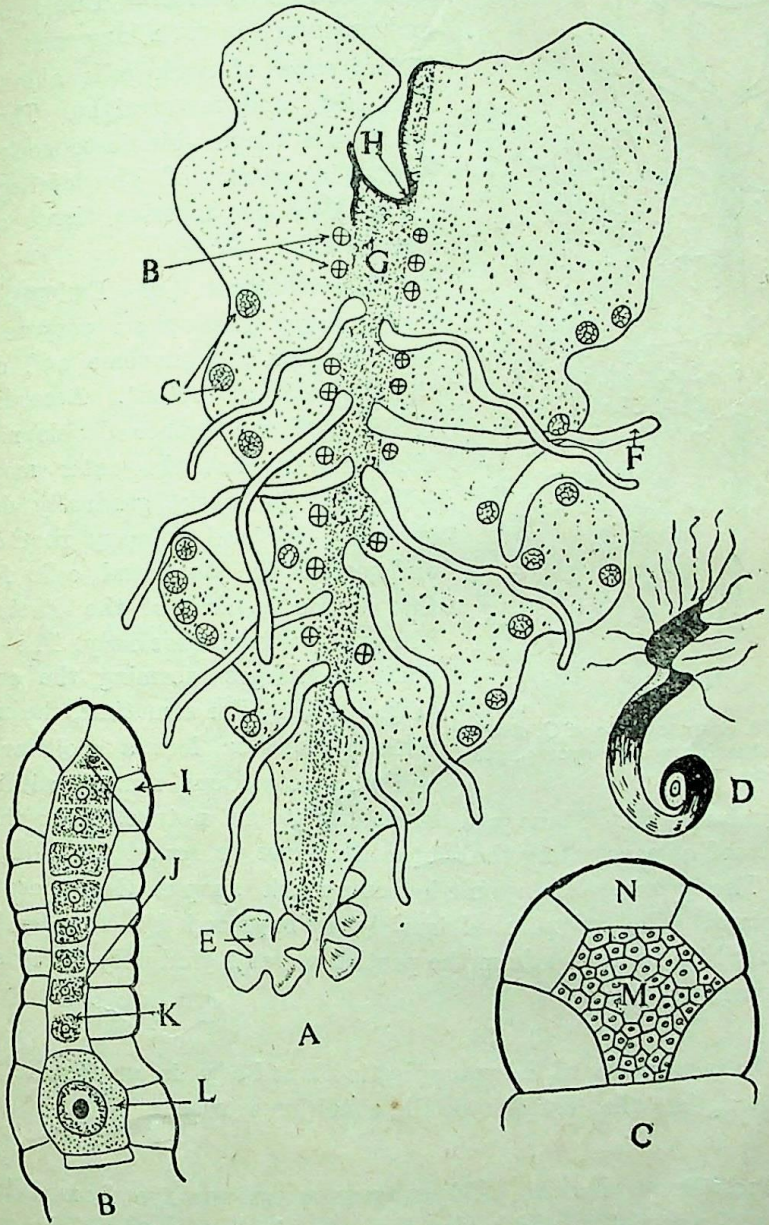

FIG. 105. Mature prothallus of *Osmunda regalis* showing anthoridia and archegonia on the ventral side. *A*, Prothallus; *B*, Archegonium; *C*, Antheridium; *D*, Sperm; *E*, Adventitious buds; *F*, Rhizoids; *G*, Mid-rib; *H*, Growing point; *I*, Neck; *J*, Neck canal cells; *K*, Venter canal cell; *L*, Egg; *M*, Spermatocyts; *N*. Antheridial jacket.

Development of Archegonium. The archegonial initial, develop on the ventral side on or near the mid-rib,

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The **archegonia** lie horizontally with their necks parallel to the lower surface of the prothallus. The details of the archegonium development are similar to those of *Ophioglossum* and *Dyopteris*. But here the archegonium has got a long **neck** formed of four rows of neck cells about 6—8 tiers high and is straight. The neck possesses a single binulcate **neck canal cell**. The **venter** of the archegonium are sunk in the massive tissue on the ventral side.

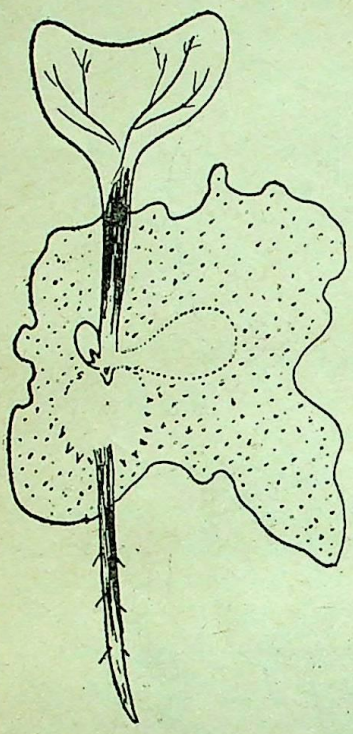

FIG. 106. Gametophyte of *O. clatoniana* showing young sporophyte emerging,

Development of Embryo. The fertilized egg develops an **oospore**. The third division is transverse and divides the oospore in octant. According to Cross (1931) the further development is abnormal in that the outer most four cells (near the neck) gradually develop the **stem, leaf** and **primary root** of the embryo and the four basal cells form a **foot** similar to that of the *Anthoceros*. The embryo develops slowly. The archegonium enlarges forming the **calyptra** (Fig. 107 Q). For sometime, the embryo remains more or less a globular mass and the cotyledous remain within the archegonium wall. These are eusporangiate in nature. But the first leaf instead of penetrating the prothallus grows up round its sides (Fig. 106). The primary embryonic leaves a much simpler than those of the adult plant. The calyptra ultimately is ruptured by the developing embryo which protrudes from the prothallus and gradually unfolds into an independent plant.

The **young stem** of the sporophytic plant body is **protostelic**. It is after a longtime that the **dictyostelic condition** is seen.

According to Brown (1920) **apogamous embryos** are formed by the activity of a meristem which develops on the lower side of the cushion of the gametophytic prothallus. This does not involve any union of gamets but a fusion of vegetative cells takes place.

Manton (1932) and Sarbadhikari (1939) have reported apospory both under natural conditions and when young sporophytes are wounded. In both cases the gametophytes are apogamous.

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Primitive Features of Special Interest in Osmunda :

1. The stem shows monostelic medullated vascular structure.
2. The main axis is dichotomously branched.

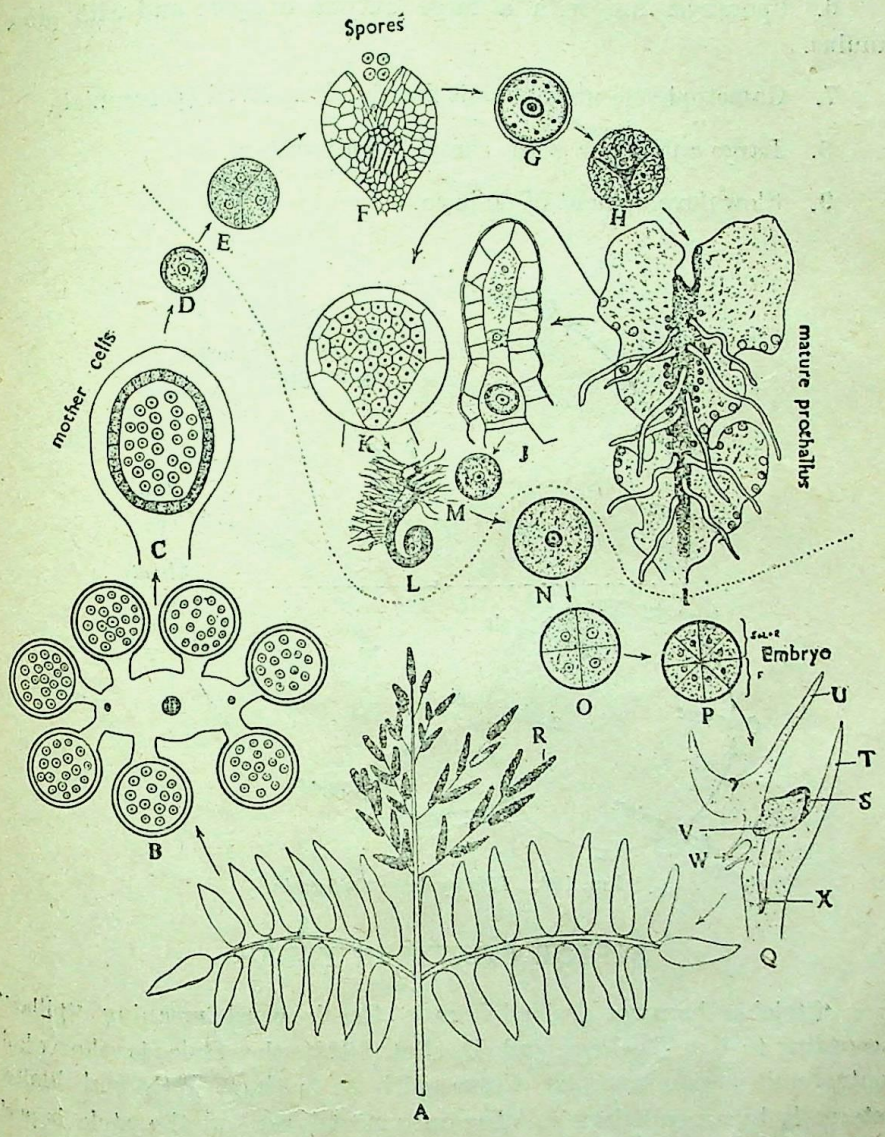

FIG. 107. Diagrammatic representation of the life history of *Osmunda*. *A*, Sporophytic plant ; *B*, T. s. of sporangiferous pinnule ; *C*, Sporangium ; *D*, Spore mother cell (2x) ; *E*, Tetrad of spore ; *F*, Dehisent sporangium showing rupture through stonimum ; *G-H*, Spore ; *I*, Prothallus showing antheridia and archegonia ; *J*, mature archegonium ; *K*, In antheridium ; *L*, Sperm; *M*, An egg ; *N*, Oospore (2x) ; *O-P*, Development of embryo. Upper epibasal cells develop stem (s) Leaves (L) and Root (R); Lower hypobasal cells develop only Foot (F) ; *Q*, Vertical section of the prothallus and attached embryo ; *R*, Sporangiferous pinnule.

3. The leaves show open venation and three-sided apical growth.

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4. Sori and indusia are absent.

5. The early development of sporangia show irregularity with divisions.

6. Sporangia are with a large output of spore and with proper annulus.

7. Gametophytic prothallus is massive long lived (perrennial).

8. Large antheridia with complex wall system.

9. Slow development of embryo.

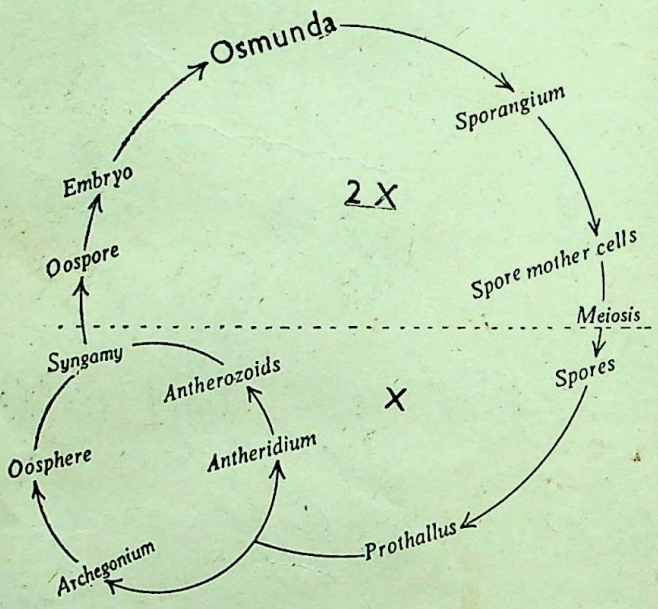

FIG. 108. Life cycle of *Osmunda*.

STELAR SYSTEM IN FERNS

'Stele' is the name derived from a Greek word meaning "pillar". According to Van Tieghem and Douliot (1886) the stele is the whole central unit mass of vascular tissue with or without pith and limited externally by an endodermis. The outermost layer of the stele is pericycle which may be one-layered or more and is formed of parenchymatous cells, within which lie one or more vascular strands formed of xylem and phloem together. The stele of the stem is connected with that of leaf by a vascular connection, known as **leaftrace**.

Steles are of five types as follows :

1. Protostele, 2. Siphonostele, 3. Solenostele, 4. Dictyostele, 5. Polycyclic stele.

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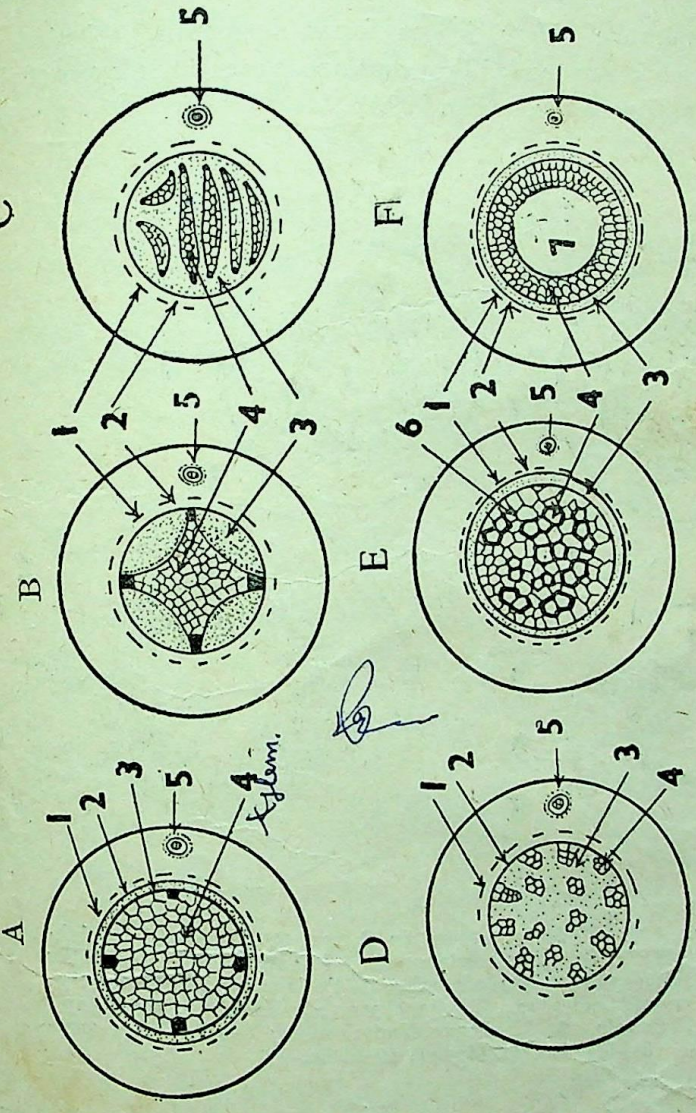

FIG. 109—I. Stelar system in Ferns. *A*, Haplostele; *B*. Actinostele; *C*, Plectostele; *D*, Mixed protostele; *E*, Protostele with mixed pith; *F*, Ectophloic siphonostele.

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Protostele. According to Jeffery (1903) this is the most primitive simplest type of stele. It has got a central solid core of xylem, which is followed by phloem and is finally surrounded by a layer of pericycle. Such a stele is seen in young sporophytic seedlings of the pteridophytes and is also seen in adult stage of certain plants like *Lygodium*, *Lycopodium*, *Glechnia* and *Selaginella*.

The protostele exists in a number of forms :

(a) **Haplostele.** Here xylem forms a smooth, spherical core which is surrounded by a continuous concentric layers of phloem *e. g.*, *Lygodium*. (Fig. 109A)

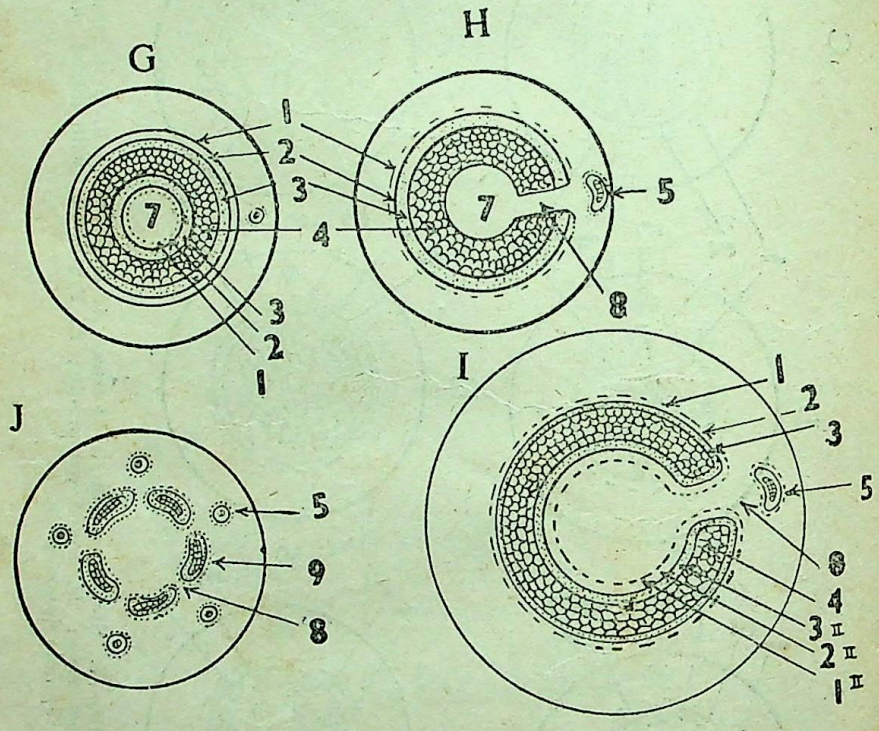

Fig. 109. II Stelar sytem in forms. *G*. Amphiphloic siphnostele ; *H*, Ectophloic solenostele ; *I*, Amphiphloic solenostle; *J*, Dictyostele ; *1*, Endodermis ; *2*. Pericycle ; *3*, Phloem ; *4*, xylem ; *5*, Leaftrace ; *6*, Parenchyme ; 7, Pith ; *8*, Leaf gap ; *9*, Merestele. 1—II Inner Endodermis ; 2—II, Inner pericycle ; 3—III, Inner Phloem ; *10*, Stele.

(b) **Actinostele.** Here the xylem is in the form of radiating ribs and the phloem is not concentric but present in isolated masses alternating with the projecting ribs of xylem, *e.g.*, *Lycopodium serratum*. (Fig. 109 B)

(c) **Mixed Protostele.** Here masses of xylem and phloem are uniformly distributed. Scattered groups of xylem elements are

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embedded in the ground tissue of phloem cells *e.g.*, *Lycopodium cernum*. (Fig. 109 D)

(d) **Plectostele.** Here the solid core of xylem gets broken in a number of plate-like lobes, more or less lying parallel to one another. The phloem alternates with xylem plates *e. g.*, *Lycopodium volubile*. (Fig. 109 C)

(e) **Mixed Protostele with Pith.** This is the modifications of a mixed protostele where thin-walled parenchymatous cells are also associated along with xylem elements *e.g.*, *Glechenia dichotoma*. (Fig. 109 E)

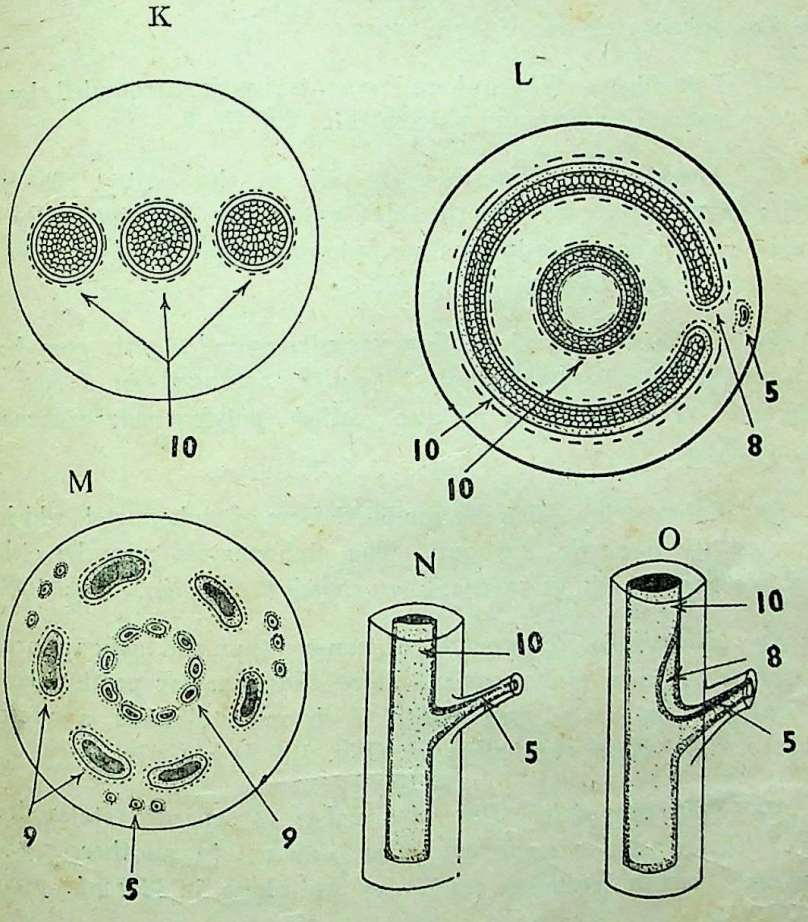

FIG. 109–III. *K*, Polystelic stem ; *L*, Polycylic solenostele; *M*, Polycyclic dictyostele ; *N*, Diagrammatic representation of the relation of leaf-trace to the stele in case of a protostele ; *O*, Diagrammatic representation of a solenostele showing a leaf gap with a leaftrace.

Siphonostele. This is a modified form of a protostele which has developed a central pith, hence often called **medullated protostele.** Here the xylem is in the form of a hollow cylinder surrounded by concentric phloem

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with pith in the central region. There are two views which suggest the manner by which the siphonostele has developed from the protostele.

(a) **Intrastelar origin of Pith.** According to this view the pith of siphonostele has developed by the transformation of xylem cells of protosteles into parenchymatous cells in the centre.

(b) **Invasion of cortical tissue.** According to this view (which has not received much recognition) the parenchmatous cells internal to the xylem and phloem are cortical in origin and that they have originated by an invasion of the cortical cells.

The siphonostele are of three types :

(1) **Ectophloic.** Where there is a central pith surrounded by concentric cylinders of xylem and phloem (Fig. 109 F)

(2) **Amphiphloic.** Here there is pith in the centre. The xylem cylinder is surrounded on both sides externally and internally with cylinders of phloem which in turn are followed by pericylic cylinders and endodermis. *e. g., Marsilea.* (Fig. 109 G)

(3) **Eustelic.** Here the hollow vascular cylinder pith goes broken into a number of collateral vascular bundles, arranged in a ring *e. g., Equisetum.* This structure is also called **polyfascicular-siphonostele.** (Fig. 109 K)

(4) **Solenostele.** This is a modified form of siphonostele which gets perforated by a single leaf-gap. The siphonostele may be either of ectophloic or amphiphloic nature. *e. g , simple Pteropsida.* (Fig. 109 H)

(5) **Dictyostele.** This results when more than one leaf gaps or modifications occur in a siphonostele. Here the vascular portion between two leaf-gaps is called **meristele.** Each meristele has a protostele structure. *e. g., Pellaea rotundifolia.* (Fig. 109 J)

(6) **Polycyclic stele.** Here a number of separate steles develop more or less in regular rings or cycles, one within another, *e. g.,* two cycles are seen in *Pteridium aquilinum* and three in *Matonia pectinata* (Fig. 109 M)

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SPERMATOPHYTA

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CHAPTER 10

SPERMATOPHYTA—"The Higher Tracheophytes"

General Introduction. Of the four principal groups of Plant kingdom viz., Thallophyta, Bryophyta, Pteridophyta and Spermatophyta, the Spermatophyta are the highest evolved and extensively studied. They are higher tracheophytes and are commonly called the **"Seed Plants"** (*Sperma*=Seed+*phyton*=plant). The seed is the chief organ of propagation of these plants and conceals within it the alternation of generations of spermatophytes. Heterospory—a condition of paramount importance, has led to the origin of Seed plants. "By the term **"Seed"** is implied a structure enclosing an embryo, protected by a special covering—the seed coat or testa. A store of reserve food material is also present either in the tissue of the embryo itself or in a special tissue, the endosperm, which surrounds the embryo. A seed is formed when the ripe megaspore is not released from the megasporagium, but remains enclosed in it and there produces female prothallium, archegonia and embryo. The seed, therefore, is simply a megasporangium modified in a peculiar manner, which separates from the asexual generation and encloses the megaspore with the female prothallium and embryo".

The seed, it is said, makes civilization possible. Our ancestors learned at an early date that it was possible to gather seeds and not only use them as an intermediate source of food, but also to set aside a small portion so as to ensure the next year's crop. It is with this significance in our minds that we commence a study of seed plants.

The spermatophytes have evolved from some lower group of plants. During the course of evolution, they have completely adopted themselves to the terrestrial habit and show a marked advance over the lower group of plants. The land habit obliged these plants with the formation of various tissues for the performance of functions of all description. Complications in this process of division of labour gave rise to the giant plant bodies which are seen occupying the major part of the world today. But this giant tree-like habit is regarded as primitive condition and hence the physiological modification results in evolved herbaceous habit.

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Habit and Habitat. The sporophytic plant body may take one of the several forms. The most common is the tree habit which is shown by such plants as Pine, Oak, Palm, Peepal etc. The second type is the herbaceous form, which includes plants that range from minute size hardly seen with the naked eye, to large plants with considerable amount of woody tissues. The herbs are annual, mostly perennial. (It is believed that the herbaceous stem is a highly specialized typed and that it devoloped from the more woody tree type). The third type, is in reality a carry-over from a fern ancestry and is far less abundant than the others. In this group the plants are exceedingly fern-like in appearance and possess a dense shortened unbranched stem with a large amount of pith and large compound frondose type leaves reaching great dimensions. The characterlstic habit is seen only in cycads.

Whatever be the form, the plant body is differentiated into root, stem and leaves. These display a large number of complex variations. In most cases the leaf is an expanded blade with a fairly elaborate vascular skeleton but in many of the evergreen gymnosperms the leaf is needle-like and shows prominent xerophytic features such as seen in desert plants. The vegetative organs with a few exceptions possess vascular cambium which contributes to the secondary growth of the plant body. The stems usually show a **eustetic** structure.

Reproduction. The seed plants reproduce by sexual means. The plants are monoecious or dioecious and are heterosporous. The spore producing organs may be borne in aggregations of sporophylls forming **strobili** or **cones** as is seen in Gymnosperms or these sporophylls may be highly modified in such a manner that a new organ—the **flower** is formed as is seen in Angiosperms. The flower is strictly homologous with the strobilus of lower plants and hence a list of synonymous terms is given below so that the dual terminology may not mislead the students.

Carpel = *Megasporophyll*

Ovule = *Megasporangium*

Nucellus = *Megasporangium wall*

Embryo Sac = *Megaspore*

Endosperm = *Female gematophyte*

Stamen = *Microsporophyll*

Anther = *Microsporangium*

Pollen Grain = *Microspore*

Pollen grain = *Male gametophyte*
and pollen tube

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The evolutionary process in seed plants results in the reduction of the gametophytic generation and its enclosure within the tissues of the sporophyte. Besides this, there has been a diminution in the actual number of cells functioning as accessory to the egg. The egg is produced in an archegonium or in a remnant of an archegonium. The male gametophyte is reduced to a few sterile cells and the male gametes. Mention must be made of the fact that fertilization is no more governed by the presence of water. This involves two stages. The first stage is the **poilination** which ensures the transfer of microspores through the agency of wind and insects, to the megaspores and are held there for further germination. The second stage is the development of **pollen-tube** an outgrowth from the microspore which carries the male gametes to the egg, without exposing them to any external injury. All this is the result of adopting the terrestrial life. The gametes, except a few very primitive members, are non motile. Such a fertilization which is accomplished with the help of pollen tubes is known as **siphonogamy** and all such plants are grouped in a biological group – the **Siphonogamia**. Fertilization, therefore, takes place within the megaspore membrane usually within the multicellular female gametophyte and an embryo develops by repeated mitotic divisions. Usually, the embryo is surrounded by **endosperm**—a food storage tissue. In Gymnosperms it is a gametophytic structure, whereas in Angiosperms it is a multicellular tissue with doubtful morphological nature and is usually the result of **"double fertilizat!on"** and **"triple fusion"**.

The embryo lies dormant in the hard covering of the seed which protects it from the adverse affects of time and climate. The seeds are capable of adapting to unfavourable season and may be disseminated by the agency of wind, water or insects. On germination, the embryo of the seeds unfolds in an independent new plant.

Classification. According to Darrah (1942) the seed plants are divided into three groups as follows :

1. **Cycadophyta :** Large plants with fern-like habit, scanty wood, large pith, naked seeds and mobile sperms.

2. **Coniferophyta :** Tree-like plants with strobili well-developed wood scanty pith, naked seeds and non-motile male gametes.

3. **Anthophyta :** This includes all flowering plants. These may be herbs, shrubs or trees whose sporophylls are organised to form unisexual or hermaphrodite flowers with ovules enclosed in an ovary which after fertilization ripens to form a fruit.

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According to Arnold (1947) the Spermatophytes in the character of their seeds are divided into two classes, as follows :

	Gymnospermae (Naked seeded plants)	Angiospermae (Flowering plants) or (Closed seeded plants)
1.	Plants mostly trees	Plants may be herb, sorub or trees
2.	Xylem except Gnetales consists exclusively of tracheids.	Xylem consists exclusively of vessels.
3.	Phloem consists exclusively of sieve tubes.	Phloem consists exclusively of companion cells and sieve tubes.
4.	Companion cells absent.	
5.	Sporophylls reduced aggregated to form cones.	Sporophylls aggregated to form flowers.
6.	Cones usually unisexual	Flowers uni or bisexual.
7.	Megasporangia borne on the surface of megasporophyll.	Megasporangia (*ovules* enclosed in ovary.
8.	Archegonium present.	Archegonium unknown.
9.	Female gametophyte extensive tissue.	Female gametophyte reduced to 8 or 16 nucleak structures.
10.	Pollination is direct. The pollen grains reach the nucellus of the ovule without the intervention of stigma and styles.	Pollination is indirect. The pollen tube reaches the nucellus or megasporangium by the intervention of stigma and style.
11.	Zygote divides by free **nuclear** divisions.	Zygote divides by cell division.
12.	Number of cotyledons varies from 2 to 8.	No. of cotyledons 1or 2.

We have for the sake of convenience followed Arnold's classification in this text.

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CHAPTER 11

GYMNOSPERMAE

These are commonly called (*Gymno* = naked + *sperma* = seed) **"Naked-seeded plants"** and together with Angiosperms, compose the present day group of Spermatophyta. Goebel has referred them as **"Phanerogams withont an ovary"** and are regarded as the most primitive of all the seed plants. They are most ancient and the fossil record bears testimony that they once formed the predominant part of earth's vegetation. This class of Gymnospermae, in their method of reproduction shows indications whereby we can recognise the way in which the angiospermic flower may have evolved, though this does not imply that any living gymosperm can be regarded as an ancestor of the angiosperms.

The lower members of the gymnospermae possess ciliated male gametes, a feature which joins them to Pteridophyta. But they do not possess independent gametophytic generations and produce seeds due to the permanent retention of megaspores in the megasporangia, a feature which joins them to Angiosperms. Thus they form a bridge between the Pteridophyta on one hand, and the Angiosperms on the other.

Habit. These are all woody perennials but in size range from the tallest known trees to dwarf shrubs. A few lose their leaves in winter. They are represented by *Cycads, Ginkgo, Conifers, Gnetum* etc. The diversity of their vegetative parts is very great and that of their reproductive devices even greater. As a rule, they are **xerophytic** in habit and possess elaborate modifications to suit their hahitats. The Gymnospermae have two main structural types, the one exbibited by conifers, with much branching and small leaves, the other typified by the cycads with few branches and large frondose leaves.

Certain members of this class, such as the well-known *Sequoias* reach tremendous heights about 400 feet from the ground and measure 90 feet in girth. The tallest plant of *Sequoia*, in the whole world, stands now at North Derryville Flat in the Humboldt State, Redwood Park, California in America. If all goes well, it may well exceed 400 feet in height. Gigentism, however, has in the past lead to extinction. The geological history reveals the downfall of giant *Dinosaurs, Lycopods,*

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Horsetails, *Calamites*, etc and alas it will not be a surprise if these majestic *Sequois* meet the same fate as that of their predecessors.

Internal Structure. The vascular anatomy reveals that the central cylinder in evolved forms was of **siphonostetic** nature. This was made up of collateral mesarch bundles. The xylem is formed of tracheids and sieve tubes represent the phloem. The bundles of all perepheral connections were concentric or mesarch.

Among the gymospermae the universal feature was to eliminate the centripetal xylem, a tendency carried forward from ferns, until the collateral and mesarch bundles of the central cylinder became collateral and endarch. So early was this accomplished for the central cylinder (Stele) that a collateral endarch cylinder is a feature of gymospermae in general. As a rule, the gymosperms show a well-marked secondary growth by the activity of the primary cambium. This changes the general topogrophy of the stem. Both pith and cortex get much reduced in relative amount. This is best seen in Coniferales and Ginkgoals. The wood in such cases is dense and is known as **pycnoxylic**. The cycadales respond very feebly, if at all, to this tendency. Here the primary cambium is either short-lived or functions very slowly, and in some forms, secondary cambium produces cortical bundles, but the formation of secondary wood never prevents the formation of a large pith and an extensive cortex. Mesarch, concentric bundles are very common here. The wood is loose, soft and scanty and is called **manoxylic.**

Mention must be made of secondary wood in Gnetales where **vessels** are associated with tracheids, an abnormal feature among gymnospermae suggesting that vessels have developed from tracheids.

Reproduction. The reproductive organs are known as **cones** or strobili. These are unisexual though bisporangiate strobili develop in certain cases as abnormalities while the female cones are long-lived structures, sometimes remaining on the plants for several years before they become mature and the seeds are ripened.

The ovule is always **orthotropous** and is provided with one integument only. The integument is differentiated into three layers, outer and inner, **fleshy** and the middle being **stony** in nature. The stony layer is always strongly developed and in case of Pinaceae form the outer most superficial layer of the seed. In cycads the seed is fleshy due to the outer fleshy layer. Below the integument lies the **nucellus**. Both these outer structures, represent the **sporophyte** At the tip of the nucellus, there is minute opening—the **micropyle** within the nucellus is the female gametophyte (endosperm) containing two or more **archegonia** which have a tendency to eliminate the venter canal are neck canal cells. Each

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archegonium has got one **egg** cell. The female gametophyte follows the same sequence of development which occur in heterosporus pteridophytes but *Gnetum* is an exception in that the eggs are matured at the stage of free nuclear division, the most embryonic stage of the female gametophyte. The pollen tube grows through the tissues of the female prothallus and reaches the archegonium which awaits fertilization. The Gymnosperms afford the only example in the vegetable kingdom of a phenomenon called **meroblastic** formation of embryo where the embryo is formed from a part of the oospore. Such a phenomenon is of wide occurrence in the animal kingdom. The proembryo differentiates into three zones : outer **rosette** or haustorial, middle **suspensors** and the basal **embryonal** cells. The cells of suspensors grow out into long tubes, thus pushing the lower part of the archegonium and make their way to the food laden endosperm which is formed before fertilization. Sometimes adjoining tubes of suspensors, separate from one another and each produces at its apex a rudimentary embryo. Thus several rudimentary embryos are seen in an immature seed. This condition is known as **polyembryony**, but when mature only one embryo develops, the others degenerate away.

During the development of embryo, the endosperm increases considerably in size and finally supplants the surrounding tissue of the nucellus. It is here where a straight embryo distinctly differentiated into stem, leaves and root lies. The radicle lies towards the micropylar end whereas the plumule towards the basal end. The integument now transforms itself into a fleshy or stony seed coat. No structure like fruit of angiosperms is known here.

The seed on germination ruptures the seed coat through which the radicle comes out and gradually a young seedling plant unfolds itself. It consists of an erect stem which passes without any distinct line of demarcation into strong primary tap root which forms an extensive root system. The young stem grows vertically upwards and its growth is **unlimited** though it ceases in case of *Welwitschia*.

Classification. This class of Gymnospermae has been divided into a number of orders by different workers from time to time. But the classification is complicated as it includes many fossil forms which are extinct and are no longer represented in the present day flora. The fossils have revealed many facts concerning the status of many groups which are not expressed by living plants, hence, they are of paramount importance for classification. Those systems which seem satisfactory and are in use today may become obsolete tomorrow in view of certain new discoveries about fossils.

Bentham and Hooker (as early as 1866-83) divided them in three groups (Cycadaceae, Gnetaceae and Coniferae) and placed them between

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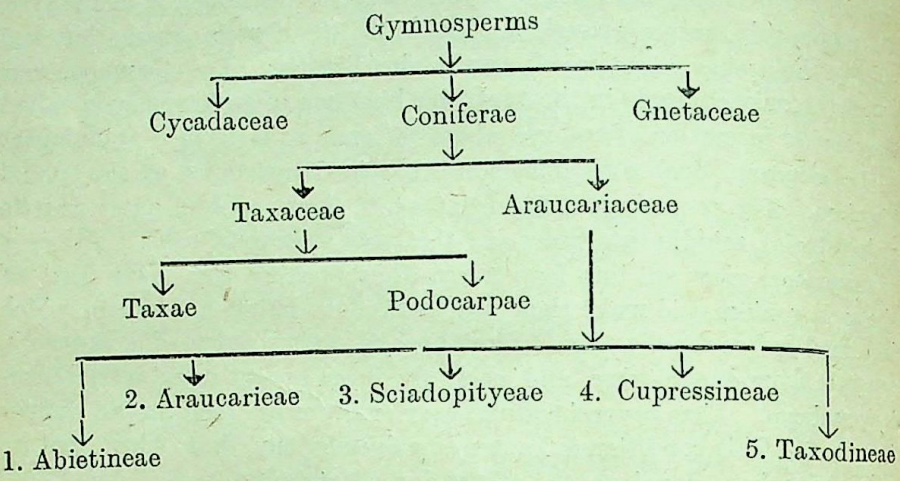
the dicots. and monocots. Eichler adopted Bentham and Hooker's classification and divided the Coniferae into Taxaceae and Araucariaceae which were further sub-divided in a number of families as follows :—



Engler (1886) divided the plant kingdom into fourteen divisions, the last was Embryophyta (Siphonogamia) which was divided into Angiosperms and Gymnosperms. The latter were divided into seven groups : Cycadofilicales, Cycadales, Bennettitales, Cordiatales, Ginkgoales, Coniferales and Gnetales. Each of the first five groups were represented by a single family whereas the Coniferales were sub-divided into seven families and the Gnetales into three.

Coulter and Chamberlain (1910) adopted Engler's system but divided the group coniferales into two families : Pinaceae and Taxaceae. The former was sub-divided into four tribes :—

Abietineae, Taxodineae, Cupressineae and Araucarineae and the latter into two tribes : Podocarpineae and Taxineae.

Chamberlain (1934) divided Gymnosperms into two complexes : Cycadophyta and Coniferophyta. The former has three orders : Cycadofilicates, Cycadales and Bennettitales and the latter has four orders : Ginkgoales, Cordiatales, Coniferales and Gnetales

Prof. Sahni (1920) divided Gymnosperms into two main Groups :

1. **Phyllosperms**—Seeds borne on modified leaf structures.
2. **Stachyosperms**—Seeds borne on stems.

The Phyllospermae, like the cycadophyte of Chamberlain include Cycadofilicates, Cycadales and Bennettitates and the Stachyospermae

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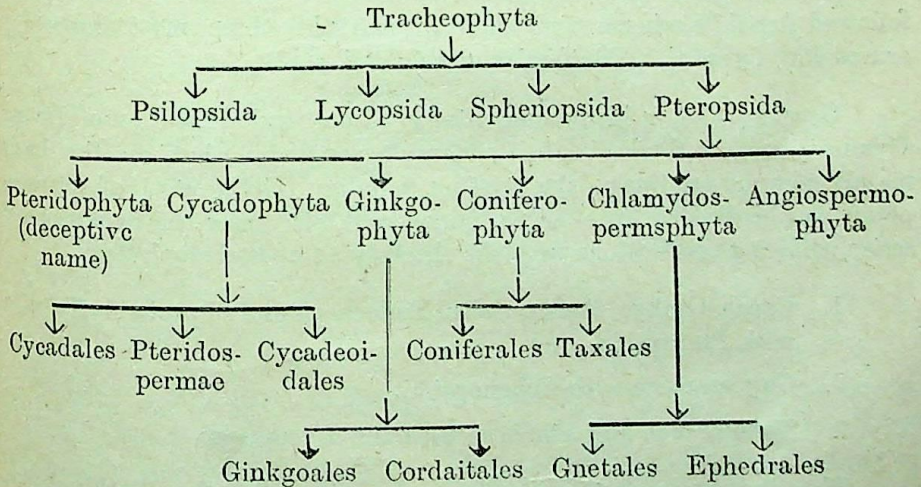
comprise all the four orders which are included in Chamberlain's coniferophyta).

Tippo (1942) divided the plant kingdom into : Thallophyta and Embryophyta. The latter have been divided into two phylums—Bryophyta and Tracheophyta. The former are divided into two classes Hepaticae and Musci and the latter (Tracheophyta) into four sub-phylums : Psilopsida, Lycopsida, Sphenopsida and Pteropsida. The Pteropsida is further divided into three classes: Filicineae, Gynmospermae and Angiospermae. The Gymnospermae has been further sub-divided into two sub-classes : Cycadophytae and Coniferophytae. The rest of the division is just as that put forth by Chamberlain *i. e.*, the cycadophytae is divided into three orders : Cycadofilicales, Cycadales and Bennettitales and the coniferophytae is divided into four orders : Ginkgoales, Cordaitales, Coniferales and Gnetales.

Professor Arnold (1948) in a symposium on 'Gymnosperm Taxonomy' pointed out that Gymnosperm as a Group has out lived its name. It can only be retained for the sake of convenience as a common name without any taxonomic status. According to him, "The members of the erstwhile Gymnospermae should then be parceled among three groups, which with ferns would constitute primary heading under the **"Pteropsida"**. His classification can be summarised as follows :—



Johansen (1951) is of the opinion that the term Gymnosperm is vulgar and should not be retained in any form, hence abondoned it altogether. He has proposed a very complex scheme according to which the various sub-class and groups of Arnold have been raised to the rank of following divisions :—

I. **PTERIDOSPERMOPHYTA**

order 1 **Cycadofilicales** (3 families)

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II. **CYCADOPHYTA**
- order 1 **Cycadales**
- order 2 **Bennettitales**
- order 3 **Nilsoniales**
- order 4 **Caytoniales**

III. **GINKGOPHYTA**
- order 1 **Cordaitales** (3 families)
- order 2 **Ginkgoales**

IV. **CONIFEROPHYTA**
- order 1 **Voltziales**
- order 2 **Coniferales** (10 families)

V. **EPHEDEROPHYTA**
- order 1 **Gnetales** (3 families)

Thus this short review of classification shows how deeply botanists disagree on the classification of Gymnosperms but all confirm to an accepted order of evolution from the lowest group of Pteridosperms to the highest evolved Gnetales. Most botanists believe that the Gymnosperms, through the transition group of Pteridosperms, represent only a more evolved phase of the pteridophytes. We have for the sake of convenience followed Arnold's scheme and shall discuss the three most important orders *viz.*, Cycadales, Coniferales and Gnetales.

Gregus (1955) in his monumental work on "Indentification of Living Gymnosperms on the basis of Xylotomy" concludes that on the basis mainly of wood anatomy, the existing families (phyla, etc.) of gymnosperms can be divided into three fairly well circumscribed evolutionary series, showing correlations with the three types of Pteridophytes :

1. Cycas, Ginkgo, Araucariales, Podocarpales and probably Taxales with Pteropsida.
2. Cupressaceae with Sphenopsida.
3. Taxodiaceae and Pinaceae with the Lycopsida.

Thus it is probable that Gymnosperms are, like the Pteridophyta, not of monophylitic but at least of triphyletie origin.

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CHAPTER 12

CYCADALES

The Cycadales is a unique group of relatively rare plants of the tropical or sub-tropical regions. The group is of special interest on account of the retention of a number of primitive characters which are possessed by no other living group of gymnosperms, that has held the attention of plant morphologist for more than a century. The following reasons are responsible for such sustained interest in them :

1. Anatomically and in leaf form they are closest to ferns of all living seed plants.

2. Their long fossil record connects them with paleozoic Pteridosperms, with which they resemble in several respects as follows :—

(a) Frond like leaves.
(b) Large leaf stalk with ample supply of supporting tissue.
(c) Thick persistent cortex.
(d) Pronounced tendency to develop anomalous secondary wood with medullary rays.
(e) Large pith sometimes containing mucilage ducts.
(f) Presence of centripetal xylem in the cone axis.
(g) Motile male gamets.
(h) Structure of ovule.

This group like Bennettitales, was derived from Pteridosperms, probably being differentiated from that group in the later Carboniferous (See Geological table page 214). Though the cycadales have not left as complete a record as may be hoped, still there is complete proof of their presence throughout the Mesozoic. There were cycad like leaves in the Permo-carboniferons. Records are more abundant in the Jurrasic and the group reached its zenith, in the Cretaceous. Then it began to decline, and now they are confined to tropical and sub-tropical regions occupying scanty patches in out of the way places, often reaching inhospitable ground where nature as well as man seen to conspire against their success. The cycads of today may rightly be called **"living fossils"** because they come down from the remote past with so little change so

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Geological time (Modified from C. R. Longwell & R. F. Flint)

Era	Rock system or Series Period or Epoch	Age in Years
Cenozoic	Pleistocene	1, 000, 000
	Pleiocene	12, 000, 000
	Miocene	(17, 000, 000)
		25, 000, 000
	Eocene	(58, 000, 000
		60, 000, 000
	Paleocene	70, 000, 000
Mesozoic	Cretaceous	130, 000, 000
	Jurrasic	165, 000, 000
	Triassic	200, 000, 000
	Permian	(230, 000, 000)
		235, 000, 000
Paleozoic	Carboniferons { Pennsylvanian	260, 000, 000
	Carboniferons { Mississippian	285, 000, 000
	Devonian	325, 000, 000
	Silurian	350, 000, 000
	Ordovician	410, 000, 000
	Cambrian	(440, 000, 000)
		500, 000, 000
Proterozoic	"Pre,cambrian"	(620, 000, 000)
		to
Archeozoic		(2, 000, 000, 000)

Note : Figures in brackets are based on determinations from radio-active minerals in rocks known to belong in the time division indicated.

that if a man, from cretaceous is brought today, he will very easily recognize the modern living forms of today (Seward). Besides this it has also been predicated that they will be extinct by the next geological era.

The cycadales, commonly called the *cycads*, include a single family *Cycadaceae* and comprises of nine living genera and about 1 0 species. All of these are typical **xerophytes**, which superficially suggest both ferns and palms, in sofar as the general form of the plant body is concerned. There is a short thick stem (trunk) crowned by a cluster of very large pinate leaves at the top. In certain cases such as in *Zamia* the stem is sub-terranean. The growth is very slow and branching is very rare. Cortex and pith are large in case of stems. The vascular tissue

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occupies a very meagre portion of the stem and is represented by conjoint, collateral, endarch and open vascular bundles. Cambium, though present, contributes very little to the secondary growth.

The plants are **dioecious**, the micro—and megastrobili being developed by different individual plants. The megasporophylls are foliar in character and are covered with ramenta. Except in *Cycas*, the megasporophylls are aggregated to form compact cones. The ovules are peculiar in that they have pollen chamber for pollen reception. The sperms are motile.

Mexico, West Indies, Australia and South Africa are regarded as the great cycad regions of the world. Out of the nine genera, four are distributed in the west and five in the east. The **Western cycads** are represented by *Dioon*, *Ceratozamia*, *Microcycas* and *Zamia*. The **Eastern cycads** are confined to Southern hemisphere and are represented by *Cycas*, *Encephalartos*, *Stangeria* and *Bowenia*.

We have taken the representative genus, *Cycas*, from which the group derives its name, for the description of life history.

CYCAS

Systematic position :

Division—*Tracheophyta*
Sub-division—*Pteropsida*
Class—*Gymnospermae*
Sub-class—*Cycadophyta*
Order—*Cycadales*
Family—*Cycadaceae*
Genus—*Cycas*.

Distribution—*Cycas* is one of the most primitive genera of world wide distribution but is more common in Australia, Africa, and East Asia. The plants are usually formed in open, sunny, well-drained habitats. Their normal size ranges from 8 to 14 feet in height. *Cycas media* is the tallest species of about 20 feet height. In India five species are commonly met with either in wild or in cultivated state. *C. revoluta*, *C. rumphii*, *C. circinales*, *C. pectinata*, *C. beddomi*. Out of these, *C. revoluta*—the **"Sago Palm"**, native to South Japan and China is widely cultivated all over the world.

Habit and External Vegetative Characters. The plant has a tuberous, unbranched, erect and columnar stem bearing at the apex a crown

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of large compound foliage leaves in apparent whorls (Fig. 110, 111). The

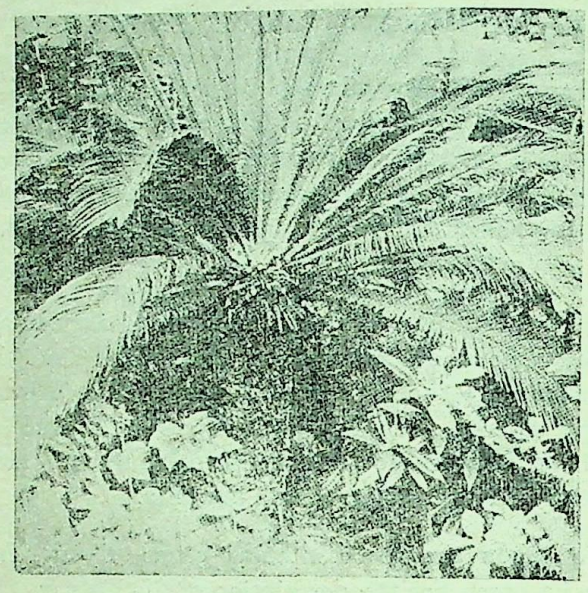

Fig. 110. Habit of *Cycas revoluta* showing a new crown of leaves with circinate pinnae.

leaflets are strong and leathery and may keep their fresh green colour for

Fig. 111. Habit of *Cycas circinalis*.

Fig. 112. Variation in the number of leaflets of various species of *Cycas* ; *A*, Leaf of *C. revolua*; *B*, leaf of *C. circinalis*.

a long time after being cut from the plant. The bases of these leaves are

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covered by woody scales which give a rough and wavy appearance to the trunk The pinnately compound leaves show circinate vernation. The rachis is straight, stiff, spiny in texture, sometimes reaching a length of 9 feet. The rachis bears two rows of leaflets. The number of leaflets varies with the species (Fig. 112). *C. circinalis* shows 80 to 100 pairs of leaflets whereas *C. rumphii* shows 50 to 60 pairs of leaflets. The leaves are spirally arranged on the stem. It has been reported that in *C. revoluta*, a new crown grows in alternate years but cases are not uncommon where a crown develops each year. The general appearance of the plant is more or less like a small palm. The plant is provided with a deep, extensive tap root sytem. Besides the normal soft roots, are present vertical aerial bunches of dwarfed, negatively geotropic, green coral-like roots the **coralloid roots**. These are closely massed, dichotomously branched and stumpy in nature. Rinke describes them as special organs for aeration. (Fig. 113)

Anatomical Structure :

Root. The normal roots display a typical dicot. structure. Their structures vary from **diarch** to **tetrarch** condition, xylem and phloem bundles are radially arranged on alternate radii ; cambium, though

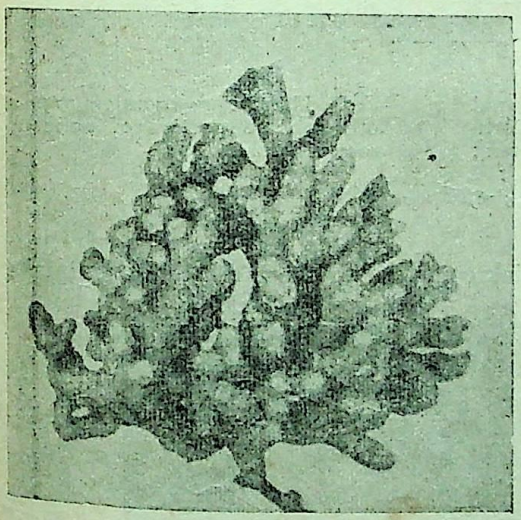

FIG. 113. A bunch of coralloid roots of *Cycas revoluta*.

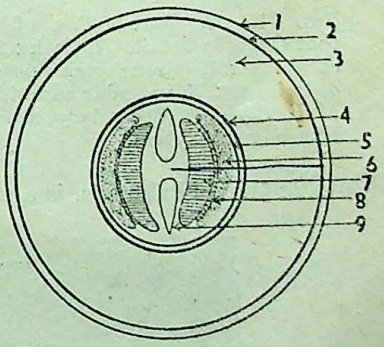

FIG. 114 Diagrammatic T. s. of normal root of *Cycas* *1*, Epidermis ; *2*, Cork ; *3*, Parenchymatus coatex ; *4*, Endodermis ; *5*, Pericycle ; *6*, Phloem ; *7*, Sec. xylem ; *8*, Cambium ; *9*, Primary xylem.

present, shows a much restricted activity (Figs. 114, 115). In the centre is a small pith. The central cylinder is enclosed by a single a layer of

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pericycle fothin-walled cells which is surrounded with endodermis.

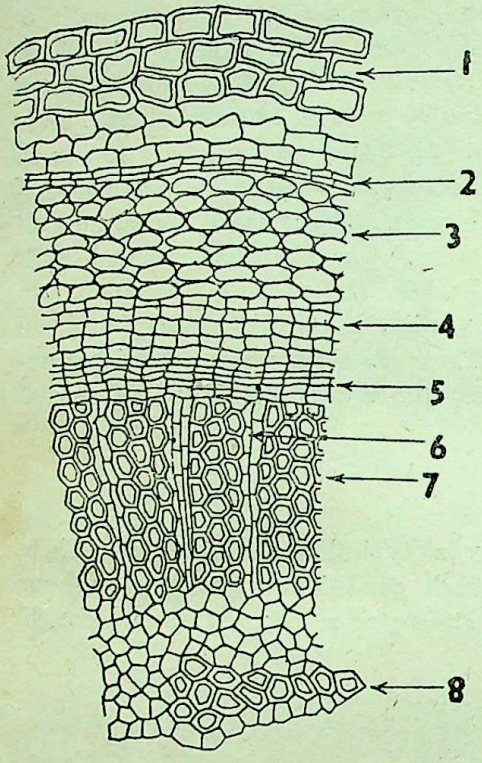

FIG. 115. A. Part of T. s. of normal root *Cycas* in detail. *1*, Cork ; *2*, Cork-cambium ; *3*, Parenchymatous cortex ; *4*, Phloem ; *5*, vascular cambium ; *6*, Med. ray ; 7, Secondary xylem ; *8*, Exarch protoxylem.

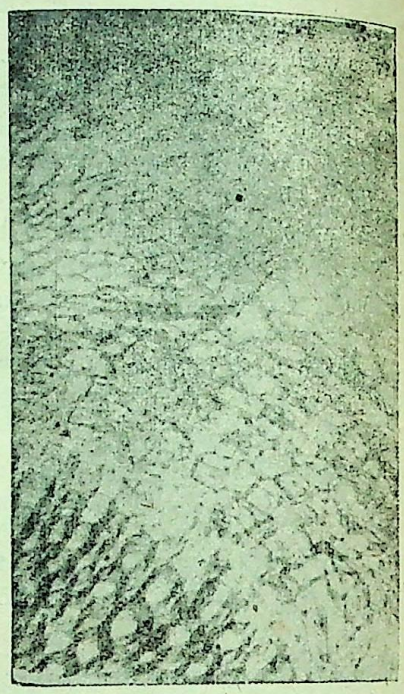

FIG. 115. B. Photomicrograph of perepheral portion of normal root of *Cycas*.

Outside the endodermis, is a thick cortex of thin-walled cells containing

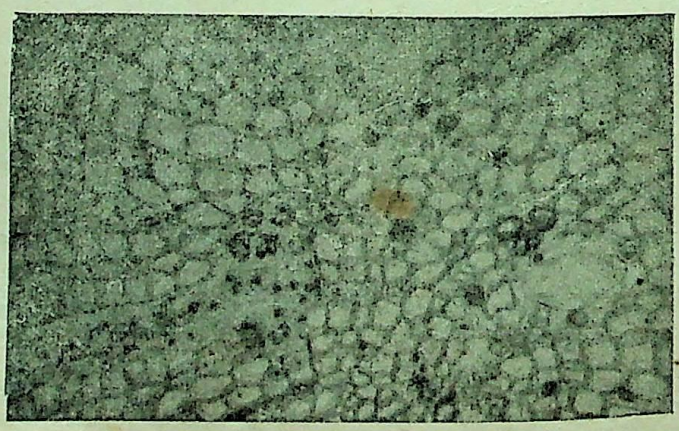

FIG. 115 C. Photomicrograph of the central region of the normal root showing a diarch primary xylem bundle.

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numerous mucilage ducts. The outermost layer of the root is the epiblema.

The coralloid roots possesses an **algal-zone** in the inner cortex, in addition to the tissues which a normal root possesses (Fig. 117). This zone is formed of large disorganised cells and contains *Anabena cycadacearum*, a blue-green alga (Fig. 116). According to Schneider (1894) some nitrogen fixing bacteria and the blue-green alga present in the root are **symbiotic** in nature. Life (1901) is of view that the algal zone serves

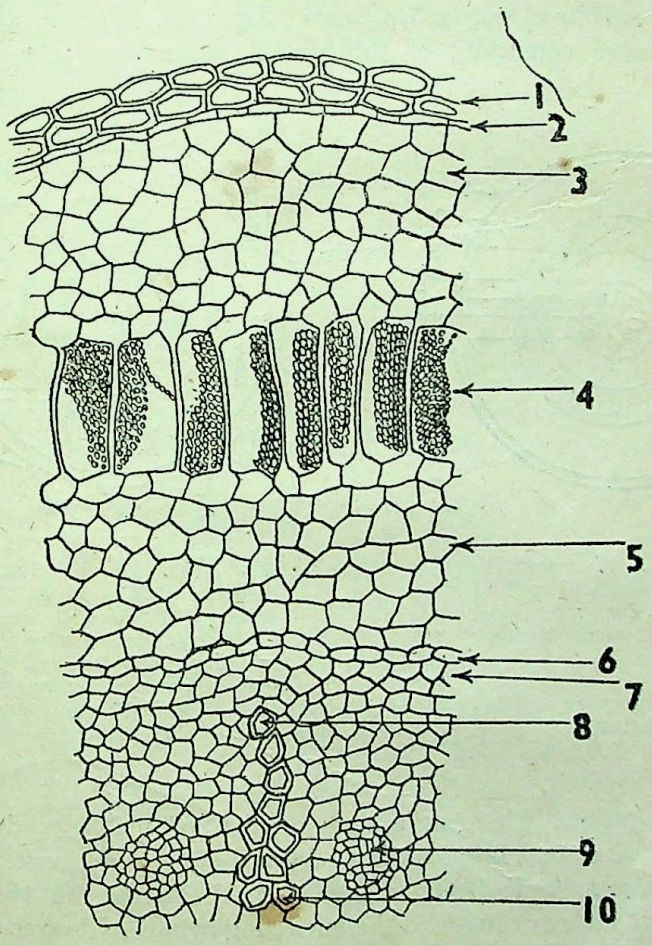

FIG. 116. Part of T. s. of coralloid root of *Cycas*. *1*, Cork; *2*, Cark cambium; *3*, Outer cortex; *4*, Algal zone; *5*, Inner cortex; *6*, Endodermis; 7, Pericycle; *8*, Exarch protoxylem; *9*, Phloem; *10*, Metaxylem.

two important functions **aeration** and **nitrification**. But Zach (1910) has discarded their symbiotic relationship and regards their association as parasitism. The observations of Schaede (1944) contradict the work of

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earlier workers. According to his observations, no bacteria are present in the coralloid roots. The earlier report about their presence in roots was due to their entry from outside by an imperfect technique. The mucus of the intercellular spaces of the root provides nourishment to the alga, which are regarded as **"innocuous parasites"** of *Cycas*. There are no conditions present in the root, which can favour free nitrogen assimilation by the *Anabena* and hence the root can not profit in nitrogen by them.

Stem. In a transverse section, the stem displays a wavy outline due to the armour of woody leafbases (Fig. 118). Cortex and pith are most extensive consisting of thin-walled parenchymatous cells filled

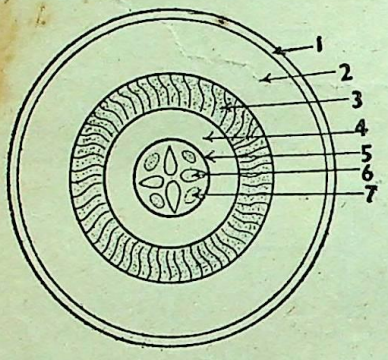

FIG. 117. Diagrammatic T. s. of coralloid root of *Cycas* *1*, Cork ; *2*, Outer Parenchymatous cortex ; *3*, Algal zone ; *4*, Inner cortex ; *5*, Endodermis ; *6*, Primary xylem bundle ; 7, Phloem bundle.

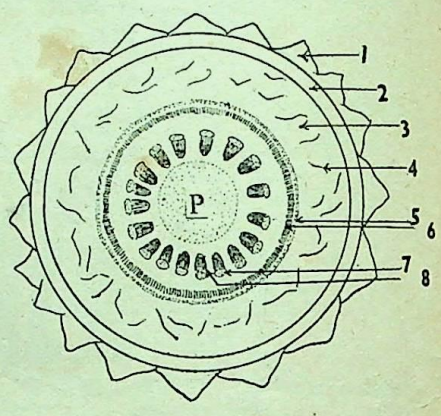

FIG. 118. Diagrammatic T. s. of stem of *Cycas*. *1*, Armour of woody leaf bases ; *2*, Periderm ; *3*, Cortex ; *4*, Girdle traces ; *5*, Phloem cylinder ; *6*, Xylem cylinder ; 5 and 6 form outer vascular cylinder ; 7 & 8 First Phloem and xylem cylinder, P, Pith.

with starch grains. There are a large number of mucilage ducts which appear as dark dots. Besides the ducts in the cortex a large number of leaf traces also make their appearance. The leaftraces are the branches of the central stelar cylinder to the encircling whorl of leaves. For each leaf there are usually four traces, two of them appear directly in front of the leaf bases and are called **direct traces,** opposite to these direct traces, on the otherside of the central cyclinder, is the place of the origin of the **girdle traces** (Fig. 119) which girdle round the central cylinder in the cortex, hence the name given. Like ferns, a leaf-gap is produced whenever a leaf-trace is given off. Since each whorl consists of number of leaves, it is not easy to get a clear picture of these in a transverse section.

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The stele is surrounded by a single-layered endodermis below which lies an inconspicuous pericycle. Within this are arranged a large number of conjoint, collateral, endarch and open vascular bundles. The phloem consists of sieve tubes only and is followed by cambium which in turn is followed by xylem formed of elongated tracheids. The primary vascular cambium is short lived, hence the secondary growth is not vigorous. Secondary growth takes place by the formation of a secondary vascular tissue. After sometime, this dies and may be superseded by a third. The last cambium has been reported to produce concentric bundles. No annual rings are formed in *Cycas* The

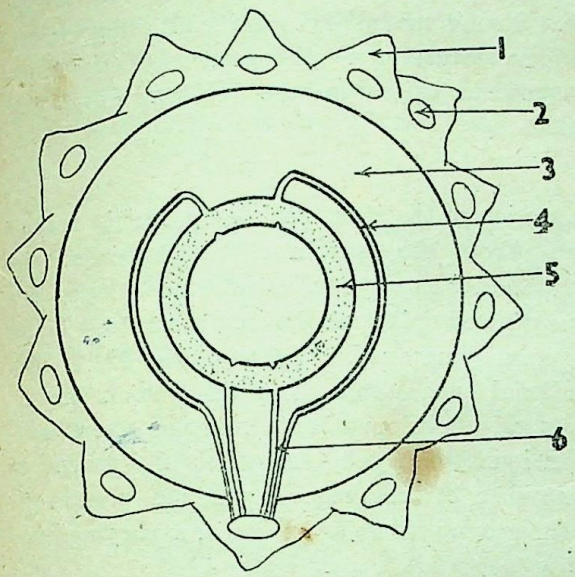

FIG. 119. Diagrammatic T.s. of *Cycas* stem showing the origin of leaf traces 1, Leaf base ; 2, Leaf-trace ; 3, Cortex ; 4, Girdle trace ; 5, Vascular cylinder ; 6, Direct trace.

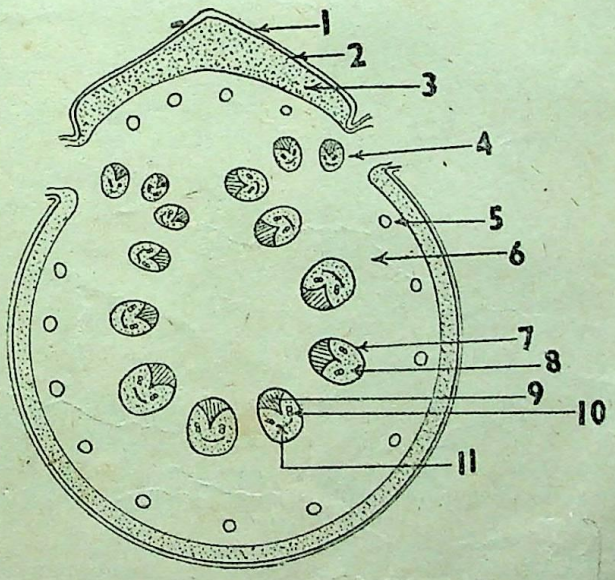

FIG. 120. Diagrammatic T. s. of Rachis of *Cycas* showing vascular bundle arranged in omega-shaped manner. 1, Cuticle ; 2. Epidermis ; 3, Scl. hypodermis ; 4, Vascular bundles going to pinna; 5, Mucilagenous canal; 6, Ground tissue; 7, Bundle sheath ; 8, Phloem ; 9, Centripetal xylem ; 10, Centrifugal xylem ; 11, Cambium.

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concentric rings of secondary tissues give a **polyxylic** structure, but these do not correspond to season growth. Hence the vascular supply is surprisingly small, hardly 5 to 10 mm. in diameter. The soft, scanty wood is known as **manoxylic**. Strong medullary rays containing **"sago Starch grains"** are the prominent feature, hence the plant is called, "*Sago-palm*". Like dicots. cork-cambium arises in the cortex developing about 10 cm. thick periderm.

Rachis. A transverse section of the stout petiole or rachis reveals a biconvex outline (Fig. 120). From the margin of the upper adaxial part the leaflets obtain their vascular supply. The outermost layer is a thick single-layered, heavily cutinized epidermis having stomata. Below this lies a few-celled thick sclerenchymatous hypodermis (Fig. 121A) This is 2 to 3 cells thick on the adaxial surface and many cells thick on the abaxial surface, whereas it is poorly developed in the margins where leaflets arise. Within the sclerenchymatous hypodermis, lies the parenchymatous ground tissues. A number of mucilage canals are seen in its perepheral region. Within the ground tissue are present, a varying number of vascular bundles arranged in a **horse-shoe** or **omega-shaped** manner,

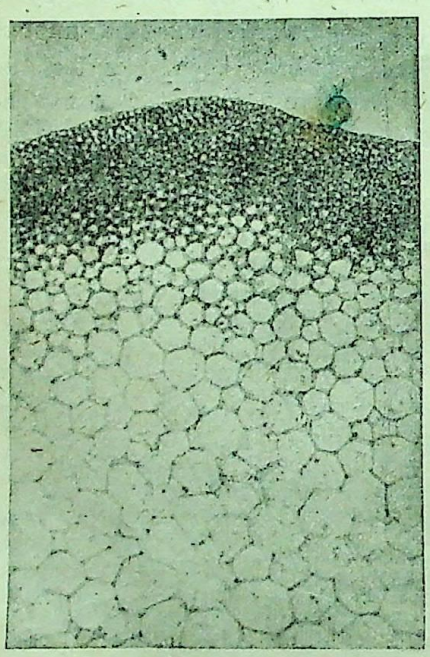

FIG. 121 A. *C. revoluta* Photomicrograph showing a portion of T. s. of petiole perepheral region.

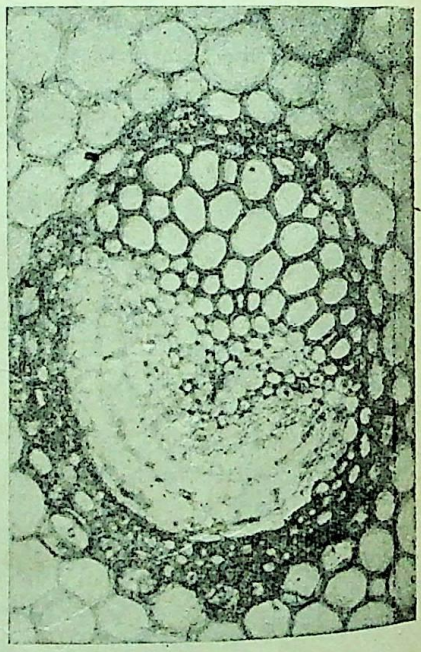

FIG. 121 B. *C. revoluta* Photomicrograph showing a vascular bundle in detail. Note the diploxylic xylem differentiated into centripetal and centrifugal type.

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Each oval vascular bundle has got a sclerenchymatous sheath within which lies pericycle of variable thickness ranging from one to many cells. This is followed by xylem cambium and phloem. The vascular bundles are conjoint, collateral and open. The xylem is **diploxylic** in that it is differentiated into **centripetal** and **centrifugal** types (Fig. 122) as shown by sections of the same petiole at different levels (Fig. 121 B). Thus the bundles reveal a different structure at the base, centre, and the apex. At the

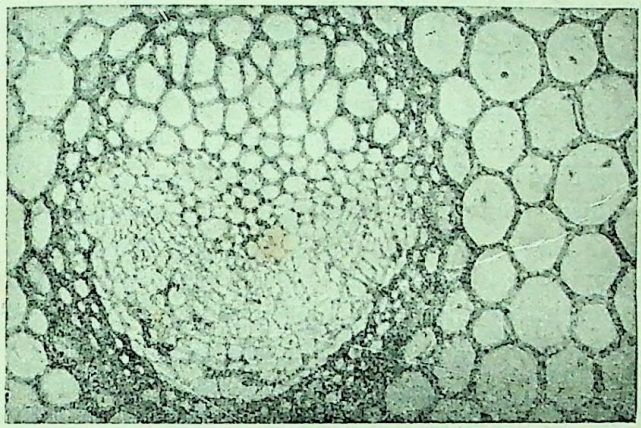

Fig. 121 C. Photomicrograph showing details of phloem in a rachis bundle and some ground tissue cells.

base, the rachis shows endarch bundles (Fig. 122). The protoxylem points towards the centre of the rachis. The meta-xylem develops from the centre, and is known as **centrifugal**. The cambium lies at the upper

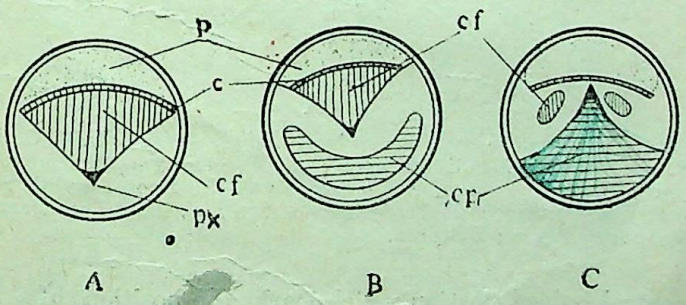

Fig. 122. Range of vascular bundles in the rachis at different levels *A*, at base; *B*, in the middle; *C*, at the apex. (P=Phloem; C=Cambium; cf, centrifugal xylem; cp, centripetal xylem, px=protoxylem.)

surface of the centrifugal metaxylem. The phloem lies above the cambium. Near the middle of the rachis, the vascular bundles show

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pseudo-mesarch structure in that some metaxylem tracheids develop, opposite the protoxylem groups. These are designated as **centripetal** metaxylem. This is formed in response to a functional change in the structure of the parenchymatous cells opposite the protoxylem. Hence the two metaxylems are of different origin. The centrifugal metaxylem develops from the plerome of the apical primary meristem. If sections are cut slightly above the middle region, a cambium develops between the centripetal metaxylem and parenchymatous pericycle.

At the apex, the rachis shows exarch bundles. Here the centrifugal metaxylem is reduced to twe small groups of few tracheids only and the protoxylem, instead of pointing towards the centre, points towards the outside *i. e.*, **exarch**. The main bulk of metaxylem is of tracheids formed of centripetal origin. The cambium lies below the centrifugal metaxylem patches and is followed by phloem which all along remains towards the lower abaxial side.

Thus from base to apex the vascular bundles show a range from endarch to exarch through intermediate pseudo-mesarch forms.

Leaflet. The leaflet, in a transverse section, reveals typical **xerophytic** characters. In case of *C. revoluta* the section shows curved or revolute margins and hence the name given (Fig. 123). In case of *C. circinalis* the margins are flat. Whatever the case may be, the leaflet

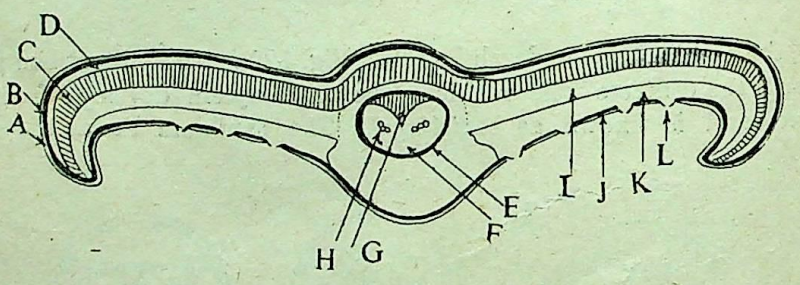

Fig. 123–1 Diagrammatic T.s. of leaflet of *Cycas revoluta*. *A*, Cuticle *B*, Epidermis ; *C*, Palisade tissue ; *D*, Sclerenchymatous hypodermis ; *E*, Bundle sheath ; *F*, Phloem ; *G*, Centripetal xylem ; *H*, Centrifugal xylem ; *I*, Transfusion tissue ; *J*, Lower epidermis ; *K*, Spongy tissue ; *L* Stoma.

shows a central bulged portion which marks the position of a single prominent **mid-vein**. On the outside is a thick layer of **cuticle** which protects the thick-walled continuous upper **epidermis** from dessication and hence reduces transpiration. This is followed by sclerenchymatous **hypodermis** which is continuous in case of *C. revoluta* though more thick in the region of midvein ; whereas in *C. circinalis*, it is confined only to the budding region of midvein and the edge of the leaflet. The sclerenchymatous

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hypodermis serves as a heat screen in protecting the plant from excessive transpiration. The **mesophyll** tissue is very well differentiated into upper elongated chlorenchymatous **palisade** cells and lower loosely arranged chlorenchymatous cells forming the **spongy** tissue (Fig. 124 A). This serves as the aerating and assimilatory tissue. The air spaces of this region communicate with the outside through the stomata. The mid-vein of the leaflet shows a pseudo-mesarch vascular bundle which is bounded

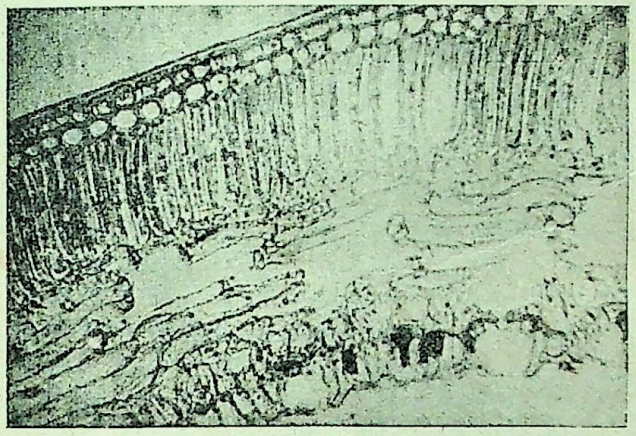

FIG. 124-A. Photomicrograph of the leaflet of *Cycas*

by a thick-walled endodermis. This is followed by parenchymatous pericycle. The **xylem** is differentiated into a broad triangular **centripetal**

FIG. 124-B. Photomicrograph of the leaflet showing a magnified view of sunken stoma.

xylem and **centrifugal** xylem in the form of two patches below it (Fig. 124 C). The protoxylem points towards, the lower epidermis and is

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surronuded by centripetal and centrifugal patches of metaxylem. Below the patches of centrifugal xylem lies **cambium** and this is followed by **phloem**, which is confined to the lower part of the vascular bundle. The

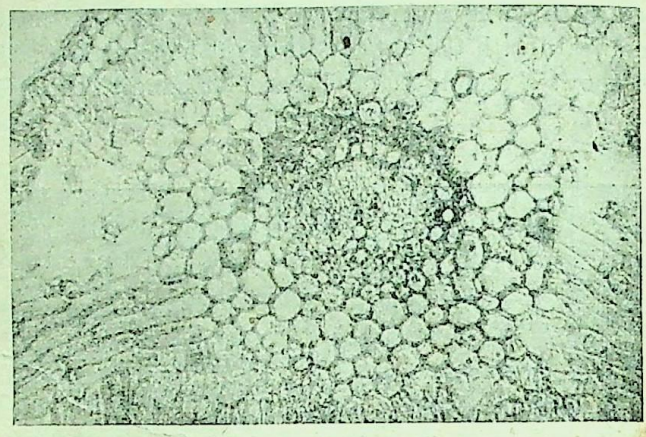

FIG. 124 C. Photomicrograph of the Midrib of *C. revoluta*

remaining space of the vascular bundle is occupied with parenchyma. On either side of the vascular bundle are strands of bast fibres. The vascular bundle is embedded in compact parenchymatous ground tissues which are impregnated with crystals of calcium oxlate. From this region rows of colourless elongated cells run laterally between the upper palisade and lower spongy tissues. This tissue is known as the **transfusion tissue** and compensates for the unbranched nature of the mid-rib. The lower epidermis, except the mid-rib, is punctured with minute-dome, shaped **pits** containing the **sunken** stomata (Fig. 124 A, 124 B). The pits are formed by the extremely thick-walled epidermal cells around the stoma which extend downwards. At the base of the pit are two **buffer cells** and guard-cells which regulate the opening and closing of stoma.

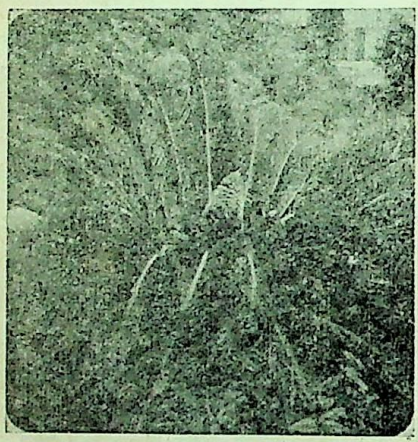

FIG. 125. Male plant of *cycas revoluta.*

Reproduction. *Cycas* reproduces by vegetative and sexual means. Asexual reproduction is unknown.

Vegetative. It takes place by adventitious buds or **bulbils**, which develop on the stem in the crevices of the scales. These are formed as a result of the hypertrophy of the cortical parenchyma and some times

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gives an illusion of a branched stem as in *Cycas rumphii*. The bulbils have few scales and foliage leaves, and when detached develop a new plant.

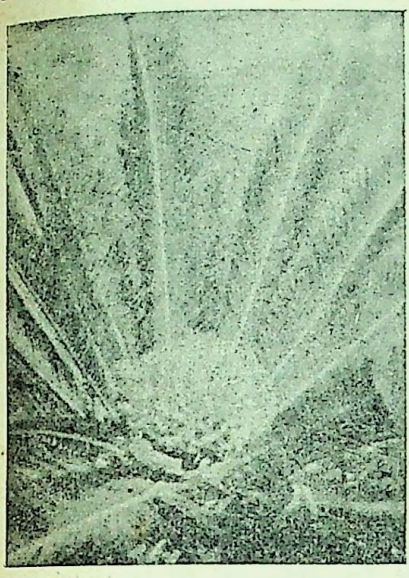

FIG. 126. Female plant of *cycas revoluta*.

Sexual. In *Cycas* and in all the seed plants, the gametophytic phases are strictly **heterothallic.** The male and female gametophytes develop from different types of spores which are called the **micropores** and **megaspores.** These develop in micro and megasporangia respectively. Both the **sporangia** are segregated in different strobili which develop on different individual plants. Thus *Cycas* is **dioecious.** Male plants of *C. revoluta* are very rare in India (Fig. 125), those of *C. circinalis* are common in Assam and Bengal. Female plants (Fig. 126) are very common in Northern India, but they do not produce any seeds and hence rightly called the "**living fossil**".

Male cone or strobilus. It develops at the apex of the stem usually singly and lies in the centre of the crown of leaves (Figs. 125, 127). It is woody wedge shaped, blunt-ended structure about 50 cm. long. Each has got an elongated axis on which the spirally arranged number of wood **microsporophylls** or stamens are attached. The microsporophyll is a flattened structure narrow below and expanded above into the expanded sterile disc drawn out in a sort of projection, the **apophysis** (Fig. 128 A). The upper portion of the sporophyll is sterile, while on the lower abaxial part **microsporangia** are borne in soral groups of three to six. The sporophylls at the base and apex of the cone are sterile. The microsporangia, which may number 700 in *C. circinalis* lie in two depressed zones on either side of a median sterile ridge and cover the entire abaxial surface of the sporophyll. The soral groups of microsporangia are surrounded by hairs. (Fig. 128 B).

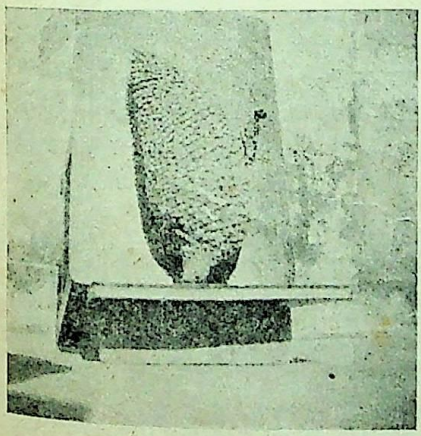

FIG. 127. Male cone of *cycas revoluta*.

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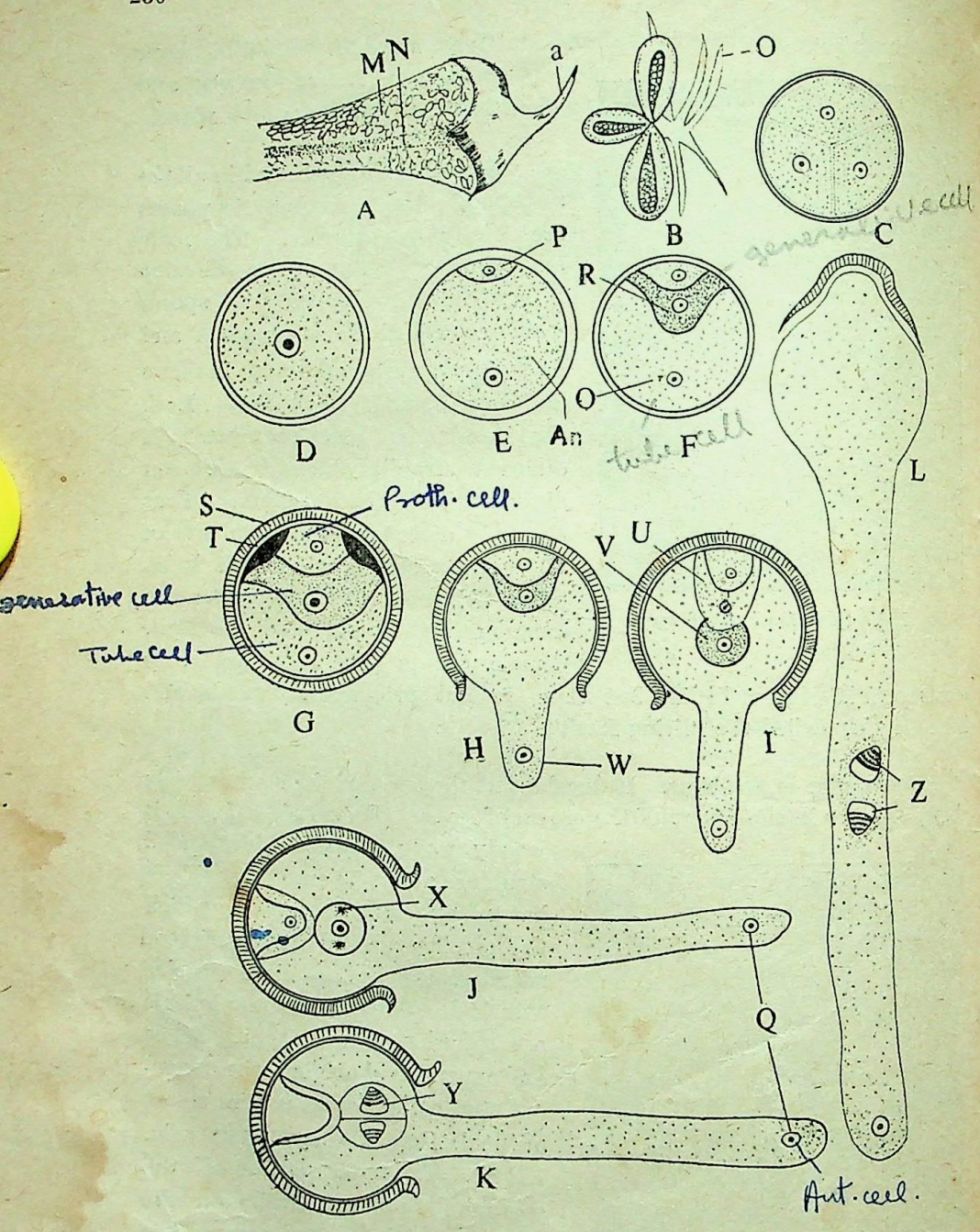

FIG. 128. Microsporophyll and development of male gametophyte of *Cycas revoluta* *A*, Microsporoplyll; *B*, Mature microsporangia arranged in groups of three discharging spores for pollination; *C*, Tetrad of microspores; *D*, Microspore; *E*, Germinating microspore; *F*, Three-celled microspore at pollination stage; *G*, Pollen grain after pollination; note the thick line about proth. cell; *H*, Development of pollen tube and bursting of exine; *I*, Division of generative cell into stalk and body cell; *J*, Development of blepharoplasts; *K*, Later stages showing sperms and elongated pollen tube; *L*, Mature male gametophyte showing elongated pollen tube, The proth. cell and stalk cells disappear. Two male sperms and a tube nucleus are seen in pollen tube; (*M*, Microsporangia; *N*, Median ridge; a, Apophyses; *O*, Hairs, *P*, Prothallial cell; *Q*, Antheridial cell; *R*, Generative cell; *S*. Extine; *T*. Intine; *U*, Stalk cell; *V*, Body cell; *X*, Blepharoplasts; *Y*, Young sperm; *Z*, Mature sperms)

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Development of Microspores and their Germination upto Pollination stage. The microsporangia are **eusporangiate** in development *i, e.*, develop from hypodermal cell of the microsporophyll. The mature sporangium is oval and attached by a short stalk at one end. The microsporangial wall is massive and four to seven cells thick. There is scanty **tapetum** below it. The **archesporium** of the sporangium develop a number of microspore mother cells which divide meiotically to give rise to tetrad of spores This marks the end of the diploid sporophytic generation and initiates the development of haploid gametophytic generation. A larger number of **microspores** are thus produced in each sporangium.

The microspores germinate *in situ*, before the sporangium dehisces. Each has got two coverings, the outer thick exine and an inner thin intine. The spore divides into a small **prothallial cell** at the lower end leaving a large **antheredial cell** (128. E). The antheridial cell divides forming a large **tube cell** and a small **generative cell** (Fig. 128 F.). As a result of the loss of water, the sporangial wall breaks open along the lower side, so that the sporangia become boat-shaped and the three-celled microspores are liberated in air for purposes of pollination. (Fig. 128 B).

Female cone or Strobilus. The genus *Cycas* is peculiar in that there is **no true female cone** or strobilus. Instead of forming a female cone, the **megasporophylls** are arranged spirally in acropetal succession forming **rosettes** or a crown (Fig. 126) leaving the apical meristem unaffected to grow and form future leaves and sporophylls. The megasporophylls develop when the plant is quite old and a crown of megasporophylls is formed each year between successive crown of foliage leaves. They are far more numerous than the foliage leaves. (Fig. 129). **The megasporophyll of *Cycas revoluta* is one of the Nature's curiosities. It preserves in a living seed plant the image of seed bearing fronds of the Paleozoic Pteridosperms".**

Fig. 129—I. Megasporophylls of *Cycas revoluta* on the female plant. Note the megasporophylls (*M*) in between the foliage leaves.

The megasporophylls differ in shape and size in different species. A reduction series may be arranged starting from *Cycas revoluta* show-

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ing all stages in the modification of foliar megasporophyll to a short woody structure in which all foliar resemblance has been lost, forming part of the cone as closely but as that of *Pinus*. Such a series will help us to know the actual course of evolution of cone in the cycads. In *C. revoluta* each sporophyll is six to eight inches long, the upper portion is broadly pinnate like a vegetative leaf and tapers to a point. On the lower half are two lateral rows of orange coloured ovules. The whole structure is covered with brown hairs. but they are lost from the ovules as they ripen. The sporophylls of *C. circinalis* are comparatively longer and has got a less number of pinnate segments whereas the pinnate segments are altogether absent in the megasporophylls of *C. rumphii*. The number of ovules also varies in different species. Only two ovules occur in *C. normandiana* and *C. siamensis*. The number varies from two to five in cases of *C. rumphii* and *C. circinalis*, whereas in *C. revoluta* the number reaches to six. The ovules of *Cycas revoluta* are the **largest** in the plant kingdom and when mature, are red in colour and may be as large as a *hen's* egg.

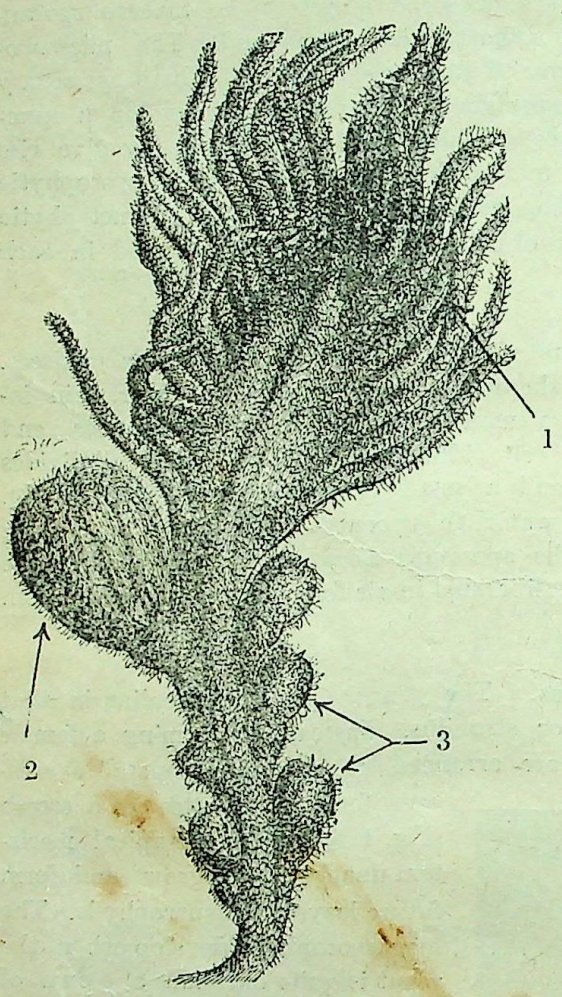

FIG. 129. B, Megasporophyll of *C. revoluta*. 1, Lobes of Carpel resembling a foliage leaf ; 2, mature ovule ; 3, Young ovule.

Megasporangium or Ovule. Each ovule has got a very thick **integument** which is in close association to **nucellus** except at the apical region where it forms a **nucellar beak** and a **micropylar opening**. Within the beaklike portion develops a hollow chamber called the **pollen chamber** (Fig. 130). When mature the integument shows

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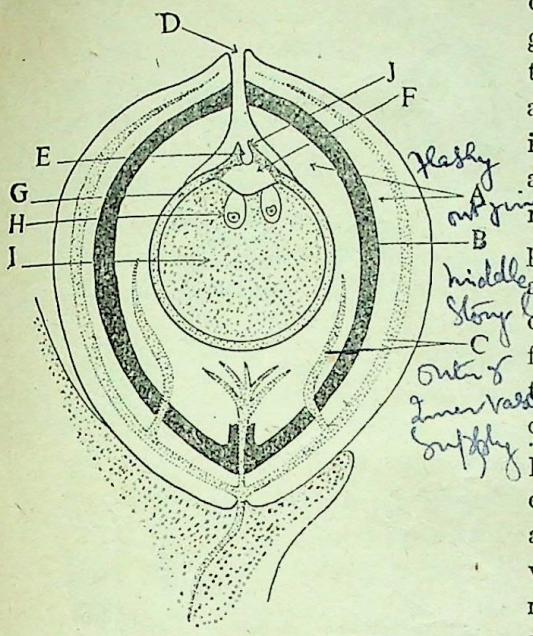

FIG. 130. L. s. of an ovule of *C. revoluta*. *A*, Fleshy outer and inner layer of the integument; *B*, Middle stony layers; *C*, Outer and inner vascular supply; *D*, Micropyle; *E*, Pollen chamber; *F*, Archegonial chamber; *G*, Nucellus; *H*, Archegonium; *I*, Female gametophyte; *J*, Nucellar beak.

differentiation into an outer green or orange fleshy layer, the middle yellow stony layer and an inner fleshy layer. The inner fleshy layer is absorbed as the female gametophyte matures and is left as a dry papery membrane closely applied to the embryo-sac. The outer fleshy layer remains fleshy throughout. Usually two vascular strands enter the ovules from the megasporophyll. The outer strand enters the outer fleshy layer and consists of about a dozen vascular bundles which extend right upto the micropyle. The second strand traverses the inner fleshy layer and consists of numerous vascular bundles.

Each ovule arises as a hypodermal mass of cells, the sterile cells about it divide rapidly so that the sporogenous cells become buried in the base of a large nucellus, around which is developed a single thick integument.

Development of Megaspore and Female Gametophyte. At first, the thin walled parenchymatous cells of the nucellus are all alike, but soon one cell in the central region becomes more prominent (Fig. 131 E). This larger cell is called the **megaspore mother cell**. It divides meiotically developing a linear tetrad of four haploid **megaspores**. (Fig. 131 I). This marks the end of diploid sporophytic generation and the initiation of the haploid female gametophytic phasess. The upper three megaspores are nonfunctional and soon degenerate forming a nourishment for the functional basal megaspore which becomes large in size at their cost. This functional megaspore is known as **embryo-sac cell** (Fig. 131 K).

Germination of Megaspore and Development of Female Gametophyte. Like megaspores of all spermatophytes, the megaspore of *Cycas* is permanenty retained in the megasporangium or ovule. It enlarges

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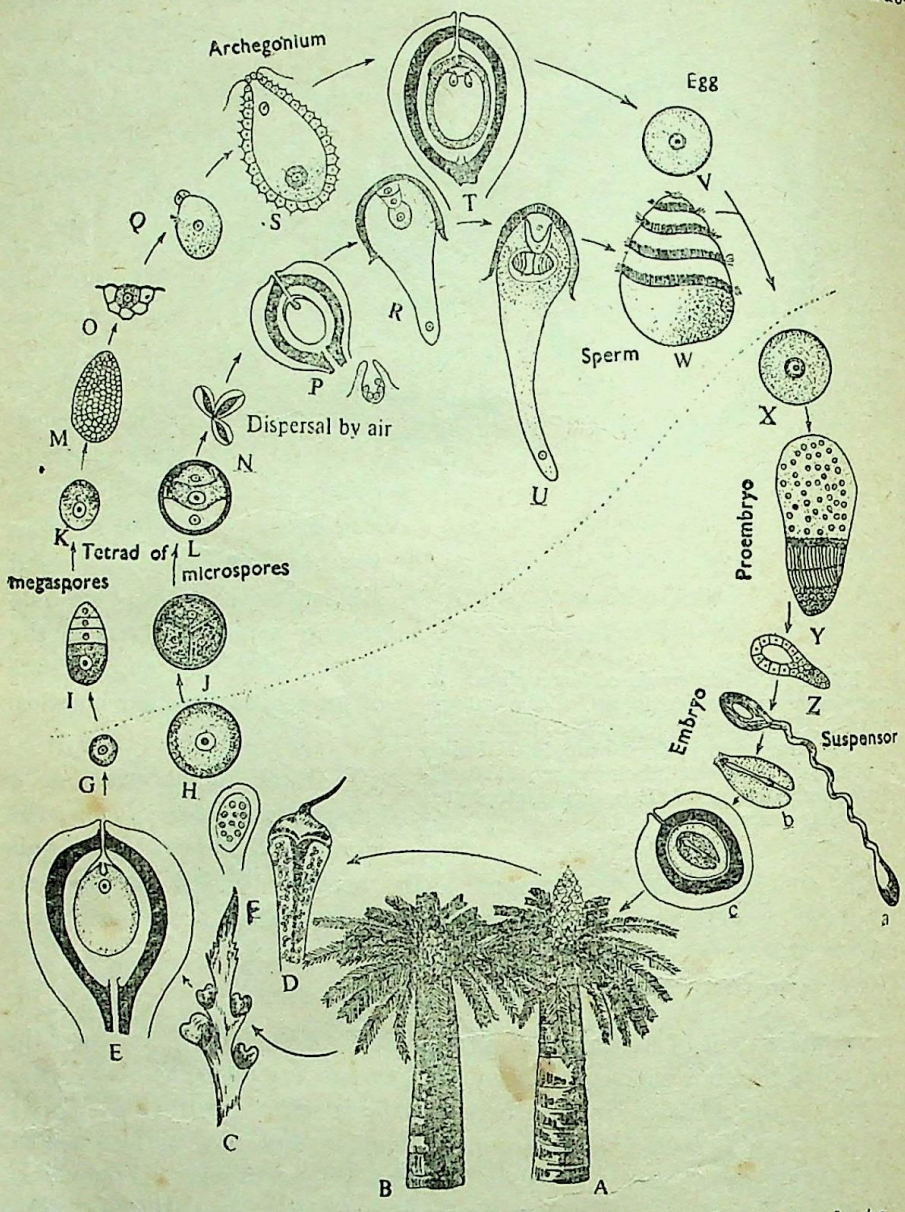
considerably and a vacuole appears in the centre which pushes the nucleus to the lower side. The nucleus divides by free nuclear division



Fig, 131. Diagrammatic representation of life-historyof *Cycas*. *A*, Male plant; *B*, Female plant; *C*, Megasporophyll ; *D*, Microsporophyll *E*, An ovule with megaspore mother cells (2x) ; *F*, A microsporangium having micropore mother cell (2x) ; *G*, Megaspore mother cell (2x) Microspore mother cell (2x) ; *I*, Linear tetrad of 4 megaspores ; *J*, Tetrad of microspore ; *K*, Embryo sac cell (x) ; *L*, Three celled Microspore at pollination stage ; *M*, Female gametophyte ; *N*, Dehiscent microsporngia liberating pollen grains for pollination ; *O*, Archegonial initial ; *P*, Pollen grains in pollen chamber on pollination ; *Q* and *S*, Development of archegonium ; *R*, Germinating microspore with pollen tube ; *T*, Mature archegonia awaiting fertilization ; *U*, Mature male gametophyte containing sperms ; *V*, Egg; *W*, Mature sperm ; *X*, Diploid oospore ; *Y-Z*, Development of embryo ; *a*, Proembryo with coiled suspensors and embryonal mass at the tip ; *b*, Mature embryo ; *c*-Seed.

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resulting in the production of more than 1000 nuclei. As free nuclear divisions continue, additional cytotoplasm is synthesized and the vacuole is gradually obliterated. At this time wall formation is initiated, lat first between the perepheral nuclei and it coninues in a centripetal direction until the female gametophyte is entirely cellular (Fig. 131 M). This is known as the **female prothallus** and consists of uninucleated cells which are smaller above and larger below. Outside this, is developed a nutritive jacket two cells thick and is called **endosperm jacket**. This seems to function like tapetum.

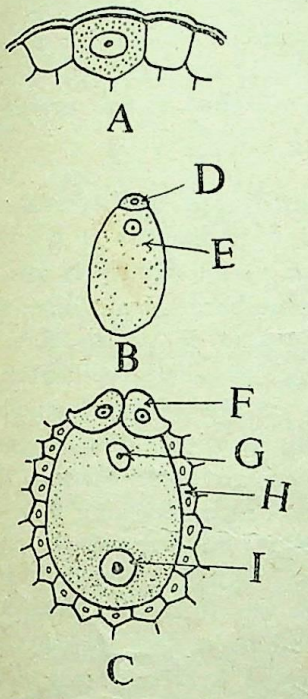

Fig. 132. Development of an archegonium of *C. revoluta*. *A*, Archegonium initial : *B*, Division of initial cell: *C*, Mature archegonium : (*D*, Primary neck cell : *E*, Primary central cell : *F*, Neck cells : *G*, Venter canal cell : *H*, Egg.)

The nucellar tissue between the pollen chamber and the female prothallus becomes soft and ultimately disorganises forming a cavity known as the **archegonial chamber.** Beneath this develop two to five **archegonial initials** each of which develops into an extremely large **archegonium**. The superficial archegonial initial divides transversly into a **primary neck cell** and a **central cell**. The primary neck cell divides longitudinally to form two neck cells which lie side by side forming a very small **neck** which projects into the archegonial chamber. The central cell, at this stage, enlarges considerably and gets surrounded with a nutritive jacket of cells called the **archegonial jacket**. Now the central cell divides to form a **venter canal cell** and a large **egg.** The venter canal cell is a short-lived structure and soon disappears. The archegonium is peculiar in that there are no neck canal cells. The egg enlarges considerably on absorbing food from the archegonial jacket. The egg of *Cycas* and its nucleus are the largest in the plant kingdom. At this stage the egg awaits fertilization.

Pollination. The wind helps to transfer some of the three-celled microspores in the micropylar region, of the ovules. At this stage some of the cells of the nucellus disorganise forming the pollen chamber and the mucilageneous product so formed fills the microphyle through which it is exuded out as a "**pollination drop**". A large number of pollen grains are entangled in this, and as it dries up, the pollen grains are drawn into

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the pollen chamber ; further drying seals the pollen chamber and the top becomes very hard. This process leaves the pollen grains to their destination.

Development of Male Gametophyte after Pollination. A week after pollination, the pollen grains germinate in the pollen chamber. The tube cell enlarges soon and this results in the bursting of the exine at the upper end and the intine comes out in the form of a **pollen tube** (Fig. 128 H). This end of the pollen grain (microspore) from which pollen tube is given off, is called **haustorial end**. This end penetrates in the nucellus so that the pollen tube grows down in the tissue of the nuceller beak serving as an haustorium. The pollen tube is not a sperm carrier. At this stage, the generative cell divides into a **stalk cell,** and a **body cell.** The stalk cell is sterile and remains attached to the persistent prothallial cell (Fig. 128 I).

No further development takes place until the archegonia are mature. For further development a period of four months is needed, after which the full grown tubes hang freely in a cavity which is partly pollen chamber and partly archegonial chamber. Meanwhile, the prothallial cell penetrates into the stalk cell, reducing it to the form of a ring. When the fertilization time approaches, the body cell enlarges enormously in the direction of the long axis of the elongating pollen tube. In the body cell two star-shaped protoplasmic bodies appear; these are known as **blepharoplasts** (128 J). They are concerned in the production of cilia and break up into a grannular mass forming five to six spiral bands. The nucleus completely divides and each of its part is attached to the centre of the ciliated spiral bands. The body-cell divides into two and thus two **antherozoids** are formed. These are liberated from the body-cell, become motile and swim actively in the pollen tube. The sperms of *Cycas* are the largest known in the plant kingdom and may attain a diameter of 300 microns and are thus visible to the naked eye (Fig. 128 K, L)

Fertilization. During fertilization, the pollen tubes are extremely turgid, probably because of high osmotic value of the substances which have been digested and absorbed by it. There is no liquid water in the archegonial chamber at fertilization time. It has been shown that the turgid end of the pollen tube bursts and discharges the sperms along with a liquid of high osmotic value. This draws water from the neck cells and from the egg, and that a portion of the egg cytoplasm protrudes into the archegonial chamber. When a sperm touches neckcells, it is sucked violently with a sufficient force so as to sever the blepharoplasts and the naked male nucleus migrates to the vicinity of the egg nucleus, which is now of tremendous size. This results in the union of male and female nuclei, the **fertilization.** This marks the culmination of sexual phases and the beginning of diploid sporophytic generation which initiates

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its development by the formation if a diploid **oospore**. This type of fertilization which is achieved by the help of poilen-tube is called **siphonogamy.**

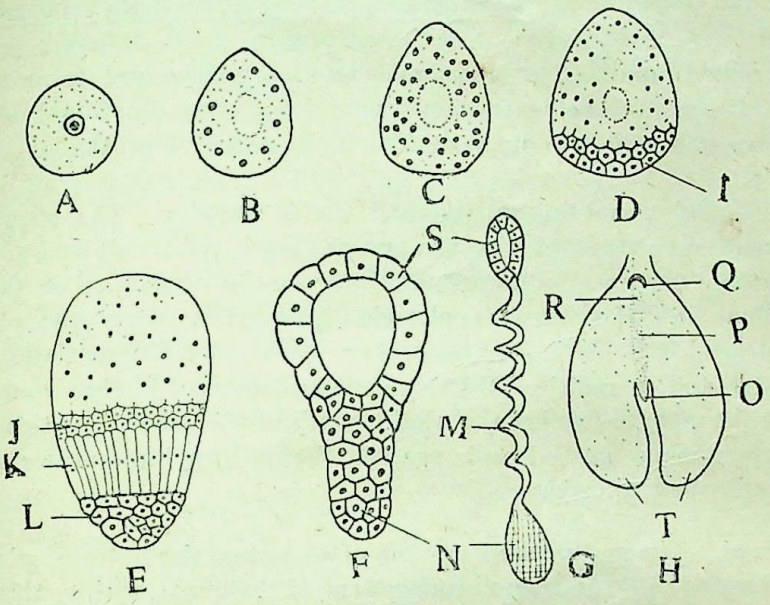

FIG. 133. Development of embryo of *Cycas revoluta; A*, an oospore ; *B C*, Free nuclear division of the zygote nucleus ; *D*, Formation of cells towards the base starts; *E*, Differention of Pro-Embryo into three regions; *F*, Proembryo with embryonal mass at its tip ; *G*, Old stage showing embryonal mass at the tip of long-coiled suspensors ; *H*. Mature embryo; (*I*, Proembryo ; *J*, Haustorial cells ; *K*, Suspensor cells ; *L*, Embryonal cells ; *M*, Elongated coiled suspensor ; *N*, Embryonal mass ; *O*, Stem tip ; *P*, Hypocotyl ; *Q*, Coleorhiza ; *R*, Radicle ; *S*, Remains of Embryonal tissue ; *T*, Cotyledons)

Development of Embryo. The diploid oospore undergoes rapid free nuclear divisions resulting in the production of about 200 to 300 nuclei. These are distributed throughout the cytoplasm of the oospore. The period of free nuclear division continues longest at the base of the oospore. Some of the nuclei in the centre along with some cytoplasm disorganise forming a large central vacuole which pushes the surviving nuclei towards the perephery (Fig. 133). Later on, wall formation is initiated among the free nuclei in the oospore near its base and extends gradually towards the neck end of the archegonium. Some of the free nuclei may remain unenclosed by walls. This region is called **proembryo** and functions as a meristematic zone.

The cells of the proembryo are differentiated into three regions : the upper region of **haustorial cells**, the central region of **suspensor cells**, and the basal region of **embryonal cells** (Fig. 133 E). The upper most region of haustorial cells is directly in contact with the free nuclear part of the oospore and serves to absorb food for the baby embryo.

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The suspensor cells elongate considerably and push the embryo cells deep into the tissue of the female prothallus. All the archegonia of one female gametophyte may be fertilized but only one embryo normally is present in the mature seed. All the suspensors from different oospores which come from different archegonia twist together and form a compound structure 'several cm. long' supporting the functional embryo. This thrusts the embryo in the middle of the nutritive prothallus.

The embryonal cells enlarge and divide rapidly. The growth, at the centre, soon stops whereas the margins grow vigorously and protrude out forming two unequal **cotyledons.** Between the depression of the two cotyledons lies the terminal **plumule**. The cells above the plumule elongate and form the axis of the embryo which soon differentiates into a **hypocotyl** and a **radicle.** Development of embryo is slow and when mature the embryo reaches the whole length of the seed. At this stage the suspensors are pushed back against the micropylar end forming a hard pad called **coleorhiza.**

Seed. The mature seed consists of an outer thick testa which is formed from the three-layered integument of the ovule, within this lie a thin layer of nucellus, the female prothallus or endosperm and a functional straight embryo consisting of two unequal cotyledons. These conceal between them a plumule. The axis of the embryo is very well marked out into hypocotyl and radicle.

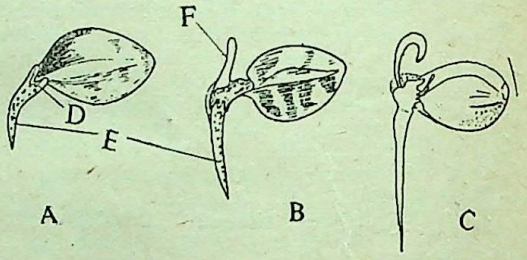

FIG. 134. Germination of seed of *C. revoluta* (*D*, Cotyledons ; *E*, Primary root; *F*, First secondary leaf.)

Germination of Seed :

The seeds of *Cycas* germinate immediately and have no resisting period. In any case, they do not keep their vitality for more than a few months. The seed coat on germination is broken up by the stony coleorhiza, which makes the passage for the delicate radicle (Fig. 134). The unequal cotyledons remain within the seed below the ground where they function in absorbing food stores in the female gametophyte cells or endosperm. When the food is finished the cotyledons dry up and are followed by the appearance of the first foliage leaf with a few leaflets. The seedling stem is very short and its vascular system forms a plate rather than a column. The seeding is an **autonomous** organization, complete in itself and the solid vascular plate is the only truly cauline stele, the plant possesses at any stage.

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Economic Importance :

Trunk of various species of *Cycas* yield thew ell-known '**sago**' of commerce, hence of economic value. A sago similar to that obtainable from palms is extacted when the plant is about seven years old (before fruiting). The plant is cut and after removing the outer bark, the core is cut into discs, sun-dried and ground into meal. On stirring the meal with water and settling, the starch separates out. About 5 lb. of sago are obtained from a stem of 4 feet long. Washed flour is used as **food** during periods of scarcity in India and Ceylon. According to Burkill and Wehmer its continuous use is said to cause intestinal troubles.

Bark and seeds of *C. circinalis* ground to a paste with coconut oil, are used as **poultice** for sores and swellings. The juice of tender leaves is said to be useful for flatulence and vomiting. The pollen is **narcotic.** The plant of *C. revoluta* is said to be a **tonic,** it promotes expectoration. Stem of c. circinates yields a **gum.**

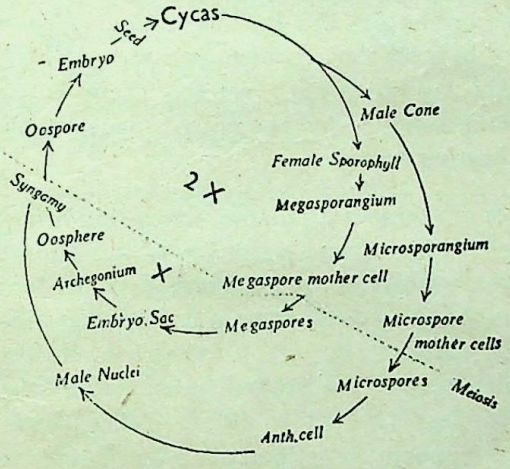

FIG. 135. Life-cycle of *Cycas*.

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CHAPTER 13

CONIFERALES

It is the largest order of the Gymnosperms, and is far more abundant than the cycadales both in the number of species and in the number of individuals, comprising about 50 living genera and 558 species. According to Buchholz (1941), thirty of the genera being confined to the Northern and fourteen to the Southern Hemisphere. Nearly all the conifers thrive best in damp mesophytic habitat and are now practically confined to lands bordering the Pacific ocean. Geologically its history does not go back beyond the Jurrasic period. Although the number of fossils far exceeds the living one, yet the group is the most dominant Gymnosperm group-today. As the name suggests, these are commonly known as **'cone-bearing trees.'**

The conifers are temperate plants, extending from arctic to antarctic regions, thriving well in tropical regions reaching the northern-most limit of tree growth where winters are so severe that the branches droop with snow. The sporophytic plants show a wide range in form. Some are prostrate though mostly are erect evergreen shrubs or trees with small leaves which persist for several years before they are shed. This order includes the largest and the oldest living trees (*Sequoias*) of the world. *Sequoia gigentica* is estimated to be of 4000 years of age with a height of 440 feet, and about 90 feet in girth. In our country, the group is very well represented in the Himalayas by various species of *Pinus* (PINES), *Cedrus* (DEODAR), *Abies* (FIRS), *Picea* (SPRUCES) *Taxus* (YEWS), *Cupressus*, *Araucarias* and *Podocarpus* etc.

Important Characteristics of the Group :

1. Evergreen plants with simple, narrow needle-like exstipulate leaves showing prominent xerophytic features.

2. The wood is dense, massive and is known as **pycnoxylic.**

3. Sporophylls arranged compactly to form a woody cone.

4. Stamens stalked bearing two or more unilocular pollen sacs on the ventral side.

5. Pollen grains may be winged as in *Pinus*, much of it is wasted.

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6. Ovules developed on the upper surface of the ovuliferous or carpellary scale.

7. Gametophytes are reduced and are entirely dependent upon the sporophyte for food and are retained within the spores.

8. Presence of non-motile male cells.

9. Polyembryony.

10. Winged seeds with an outer thick testa.

11. Seeds endospermic with a large number of cotyledons.

12. Cotyledons epigeal.

Economic Importance : From an economic stand point the order is of great importance and value as follows :—

1. Timber. Most of the plant, are of high timber value as the order is the dominant forest-maker of the world. Species of *pines*, *firs* and *red-woods* are used in building providing such items as roofing, beams, doors and window sashes. Chairs, tables and inexpensive grades of furniture are also made from such timber. (Telegraph and telephone poles, railroad ties, crates and boxes are also made from certain conifers. Pine wood forms the **'deal'** of commerce).

2. Paper. *Spruces* have been extensively used in the manufacture of pulp for paper.

3. Pencils and Penholders. The wood of *red-cedars* such as *Juniperous virginiana* has been exclusively employed for this purpose.

4. 'Naval Stores'. The wood of pines on distillation yields Turpentine, rosin, tar and pitch—the so celled **'Naval Products'** of commerce.

5. Resin. *Canada balsam*—a most important mounting specimen for biological microscopic study, is a resin from *Abies balsamia* (Balsam fir). It is also used in varnishes and certain medicinal preparations.

6. Incence. Species of *Cupressus* are used in Darjeeling and near about places for this purpose and are sold locally under the name, **'dhoop'**.

7. Food. Seeds of *Pinus gerardiana* are edible and are used in winter as dry fruits known as **'Chilgoza'** of commerce. Plants grow in North-western Himalayas and Afghanistan.

8. 'Christmas Trees'. *Spruces* and *Firs* together constitute a great bulk of the evergreens sold annually as **'Christmas—trees'** especially during Christmas and other auspicious functions.

Tanning. Bark of *Larix europea* is used for tanning purposes.

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Classification. The arrangement of genera of this group has not reached stability. A number of families and sub-orders are recognized, but their limits and the genera assigned to them vary with different authors.

According to Coulter and Chamberlain (1910) the group has been divided into two families, Pinaceae and Taxaceae. The former possesses distinct strobili whose overlapping scales protect the ovules, and whose seeds ripen dry. The latter do not possess distinct ovulate strobili, the ovules are freely exposed and the seeds may develop a fleshy testa or an aril. Both the families are sub-divided into 6 tribes in all as follows :—

Pinaceae	Taxaceae
Abietineae *e. g.*, Pinus, Cedrus, Larix, Pseudolarix, Picea, Tsuga etc.	**Podocarpineae** *e. g.*, Poducarpus, Dacrydium, Phyllocladus, etc.
Taxodineae *e. g.*, Taxodium, Cryptomeria, Sequoia, Cunninghamia, etc.	**Taxineae** *e. g.*, Taxus, Torreya, Cephalotaxus, Acmopyle, etc.
Cupressineae *e.g.*, Cupressus, Juniperus, Thuja, Libo-cedrus, Callitris, etc.	
Araucarineae *e.g.*, Araucaria, Agathis	

Pulle has divided the group into five orders which are represented by their respective families as follows :—

Order 1. **Araucariales.**
Family 1. *Araucariaceae*

Order 2. **Podocarpales**
Family 2. *Podocarpaceae*

Order 3. **Pinales**
Family 3. *Pinaceae*

Order 4. **Cupressales**
Family 4. *Cupressaceae*
Family 5. *Taxodiaceae*

Order 5. **Taxales**
Family 6. *Cephalotaxaceae*
Family 7. *Taxaceae*

We have chosen *Pinus* as the representative genus of coniferales because of the great detail in which its structure and reproduction are known and because of its widespread distribution in the Northern hemisphere.

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PINUS

Systematic position :

Division—*Tracheophyta*
Sub-division—*Pteropsida*
Class—*Gymnospermae*
Order—*Coniferales*
Sub-order—*Pinales*
Family—*Pinaceae*
Genus—*Pinus*

Distribution. There are about 75 living species of this genus. Geologically its history does not go back beyound the Jurrasic period. Usually they grow gregariously forming rather open forests. Sometimes isolated specimens on wind swept heights are seen, where their original shape is frequently altered by the influence of prevailing winds so that they become dwarfed and bent. In our country, the following species are found in N. W. Himalayas, Afghanistan, Nepal and Sikkim.

1. *Pinns roxburghii* (Pinus longifolia) **'Chil'** below 5000 feet in hills and plains.
2. *P. wallichiana* (P. excelsa) **'Kail'** or 'silver fir') between 5000 feet to 8000 feet.
3. *P. gerardiana* **'Chilgoza'** at 8000 feet.
4. *P. sylvestris* (an English cultivated variety.)
5. *P. khasya.*
6. *P. merkusii.*
7. *P. montana.*
8. *P. laricio.*
9. *P. monophylla*
10. *P. pinaster.*

Habit and External Vegetative Characters. The full grown plant of *Pinus* is a large tall tree. Usually it grows on shallow soil overlying rock, and is rooted by a well spreadout taproot system. The roots do not penetrate very deep in the soil. The main trunk is cylindrical and is covered with a rugged scaly bark. The stem branches **monopodially**, (*i. e.*, forms long lateral branches in whorls from buds developed in the axil of the scale leaves.) At the apex of the stem is a large terminal bud which grows

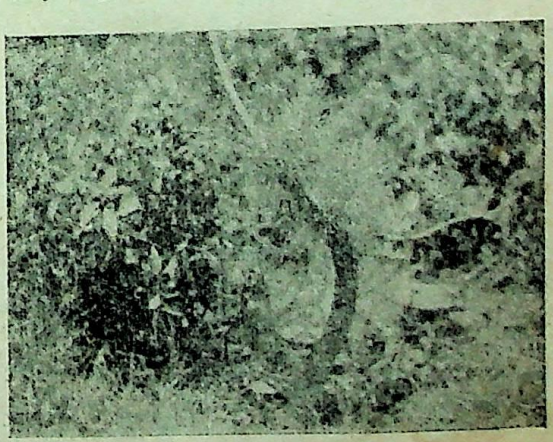

FIG. 136 A very young plant of *Pinus* showing habit

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more rapidly than the terminal buds of the branches and hence the stem tapers towards the apex forming a conspicuous central trunk. The gradual transition in length of the lateral long branches from the longest lowermost to shortest uppermost gives the tree a conical form.

In addition, to these long branches of unlimited apical growth, are given off from there many branches of limited growth—the **'dwarf-shoots'** or **'spur-branches'** or 'foliar-shoots' which develop in the axil of scale leaves. These 'dwarf shoots', have no apical buds. They possess a number of thin brown, membraneous, scale leaves below and end terminally in a fixed number of green, needle like foliage leaves. The number of such leaves produced on 'foliar-shoot' varies according to the species of the plant. *Pinus monophylla* has one single leaf, hence its spur-shoot is called **unifoliar.** *Pinus sylvestris* and *P. pinaster* are **bifoliar** having two 'needles'; *P. roxburghii* and *P. gerardiana* are **trifoliar** with three leaves; and *Pinus excelsa,* with five needles or leaves is called **pentafoliar.** Thus the leaves are of two types : Firstly green needle like **foliage leaves** ('needles') which develop only dwarf-shoots or foliar shoots and secondly the photosynthetic **scale leaves** which develop on the long-shoots and on dwarf shoots. The latter fall off as

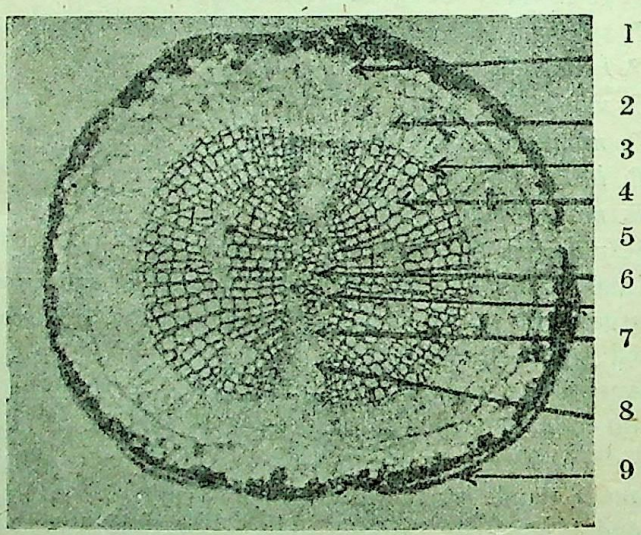

FIG. 137. Photomicrograph of *Pinus* root (T. s.) showing a diarch structure (1 Cortex ; 2. Phloem ; 3. Cambium; 4 Sec. xylem ; 5. Metaxylem ; 6. Zone of parenchymatous cells separating primary xylem from sec. xylem ; 7. Protoxylem ; 8, Resin canal ; 9. Epidermis).

the branches mature and help in conserving moisture around them. The former persist for a number of years and all are not shed at the same time thus providing an evergreen nature to the plant. They are

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shed only when the spur-shoot is shed as a whole. Thus *Pinus* produces **dimorphic branches** and **dimorphic leaves.**

Anatomical Structure

Root. It displays a simpler dicotylednous structure. When young, it is surrounded by an outermost **pileferous layer** which gives out unicellular **root-hairs** which soon disappear. Below this lies a thick **cortex** of parenchymatous cells. This is limited by a brownish layer of suberised cells containing tannin forming **endodermis** ; within this, lies a many-layered **pericycle** containing tannin and starch grains. Near the centre of the stele, lie 2 to 6, 'Y-shaped primary **xylem bundles** which alternate with equal number of phloem bundles (Fig. 138). The xylem is made up of tracheids alone and the phloem of sieve tubes and parenchymatous cells. There may be a small pith in the centre. There is a **resin-canal** between the arms of Y-shaped xylem bundle.

As the root grows older, like dicots, certain strips of thin-walled cells between primary xylem and primary phloem begin to function as **vascular cambium.** Thus the primary xylem is now completely surrounded by a ring of cambium, which develops **secondary-xylem** on its inner and **secondary-phloem** outside (Fig. 137). The outer-most layer of the pericycle forms **cork-cambium** and cuts off cork-cells on the outside which when developed sufficiently separates the cortex from the stele. The barrier of cork deprive the cortex and the pileferous layer water and food, hence they soon die and disappear. Thus, the older portions of the root are derived entirely from the stele. The second-layer of the pericycle develops **lateral roots.** The younger roots are commonly invested by a fungal growth of **ectotrophic mycrrohiza.**

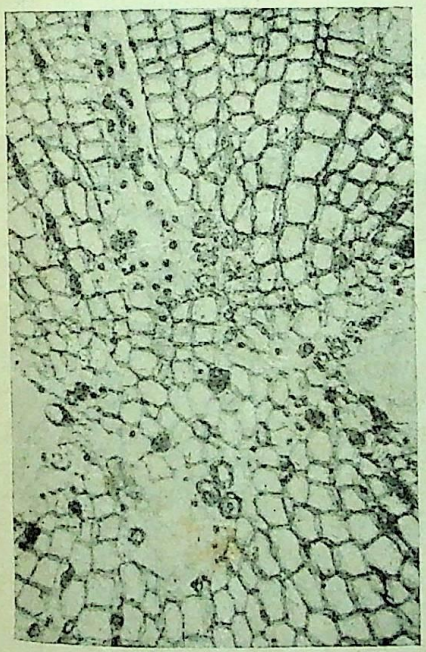

Fig. 138. Photomicrograph of the diarch primary xylem bundle of *Pinus* root. Note the primary xylem bundle is surrounded on either side by Sec. xylem. Opposite the proto-xylem lies the resin canal.

Stem. It displays a dicot structure. A young stem in transverse section shows a wavy outline. The outer surface is formed by a highly thickened cuticularised **epidermis,**

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which is followed by an equually thickened lignified **hypodermis**. Within this lies a thin parenchymatous **cortex** containing chloroplasts and resin canals which are surrounded by a glandular epilthelial cells. The stele shows **poly-fascicular siphonostelic** or **eustelic** structure. The vascular bundles are conjoint, collateral and open. They are arranged in a ring, and are separated by narrow **meduallary rays**. The phloem consists of thin-walled, elongated, more or less pointed **sieve-tubes** with **sieve-plates** on their radial walls and phloem parenchyma. The companion cells are absent. The xylem consists of **tracheids** alone. **True vessels** are **absent.** The **protoxylem** consists of annular spiral tracheids (Fig. 139, 140).

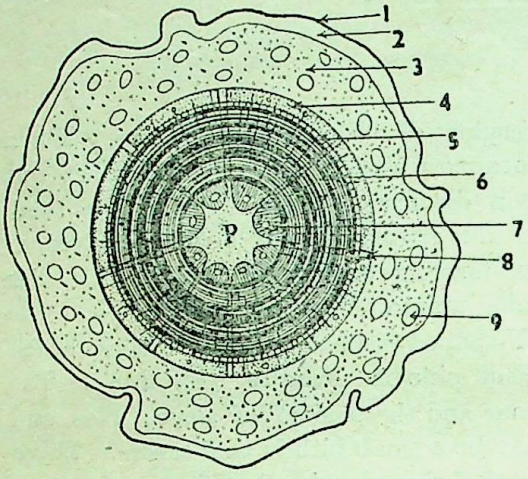

FIG. 139. Diagrammatic T. s. of *Pinus* Stem showing prominent annual rings in secondary xylem—1. Epidermis ; 2. Cork; 3. Cortex ; 4. Secondary phloem ; 5. Cambium ; 6. Sec. xylem ; 7. Primary xylem ; 8. Medullary rays ; 9. Resin canal ; P, Pith.

Secondary growth follows the course as in dicots. The vascular cambium develops **secondary xylem** and **secondary phloem**. The size of

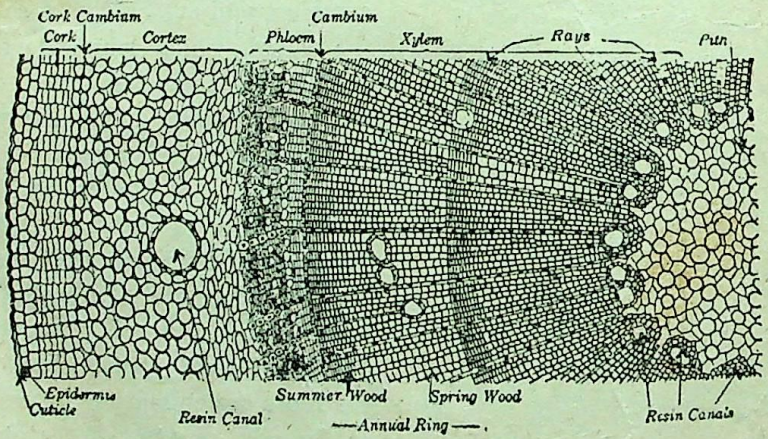

FIG. 140. Part of T. s. of *Pinus* stem.

the tracheids of the secondary xylem is much the same as that of primary xylem. Since the tracheids produced at the beginning of each growing season are somewhat larger than those developed later in the year, there are well-defined **annual-rings** in the secondary xylem

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(Fig. 141). Resin canals occur here and there in the xylem

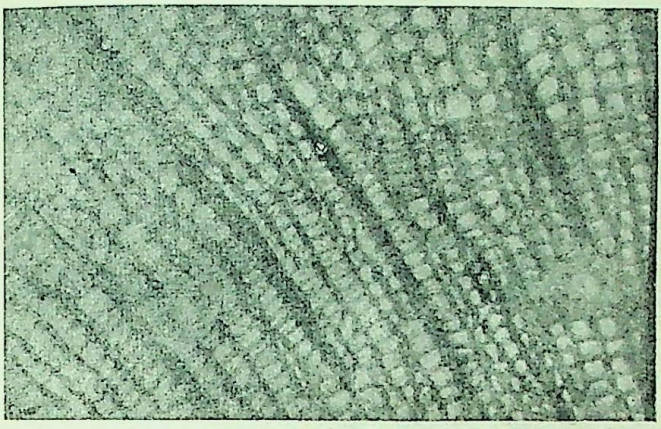

FIG. 141. Photomicrograph of a part of *Pinus* stem (T. s.) showing annual ring in Sec. xylem. Note resin canals are seen in the autumn and spring wood.

(Fig. 142). On account of the approximate uniformity in size of the tracheids and the hardness of their walls, the pine is so valuable as a

FIG. 142. Photomicrograph of the central region of the *Pinus* stem (T. s.) showing primary xylem containing resin canal, medullary ray and pith cells.

source of **lumber.** Under normal conditions, the secondary phloem remains functional only for one year, the phloem of the previous year persists as a crushed mass of dead cells on the outerside of the new living phloem. The vascular cambium develops new **secondary medullary rays** from time to time so the later-formed rings of xylem contain many more rays than do those parts of the xylem formed earlier.

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The medullary rays display a complex structure as compared to a

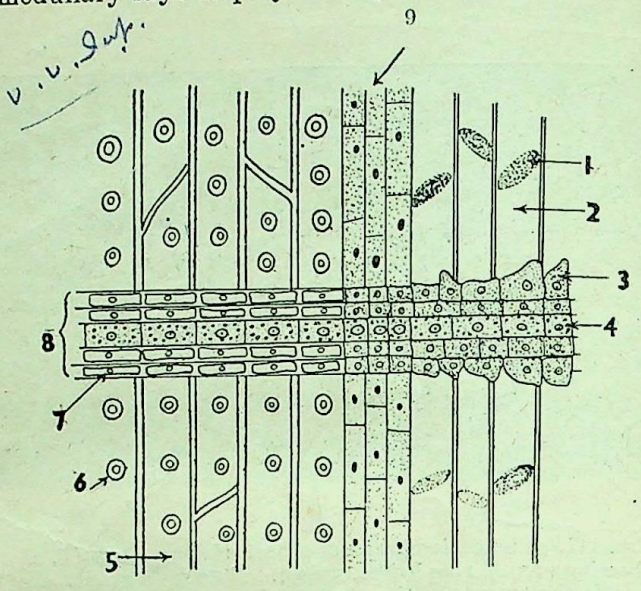

Fig. 143. Radial Longitudinal Section of *Pinus* stem showing the structure of medullary ray 1, Sieve plate ; 2, Sieve tube ; 3, Albumen cells ; 4, Starch cell ; 5, Tracheids ; 6, Bordered pits ; 7, Tracheidal cell with simple pit ; 8, Medullary ray; 9, Cambium.

dicot. Their size is variable (Fig. 143). Mostly they are uniseriate

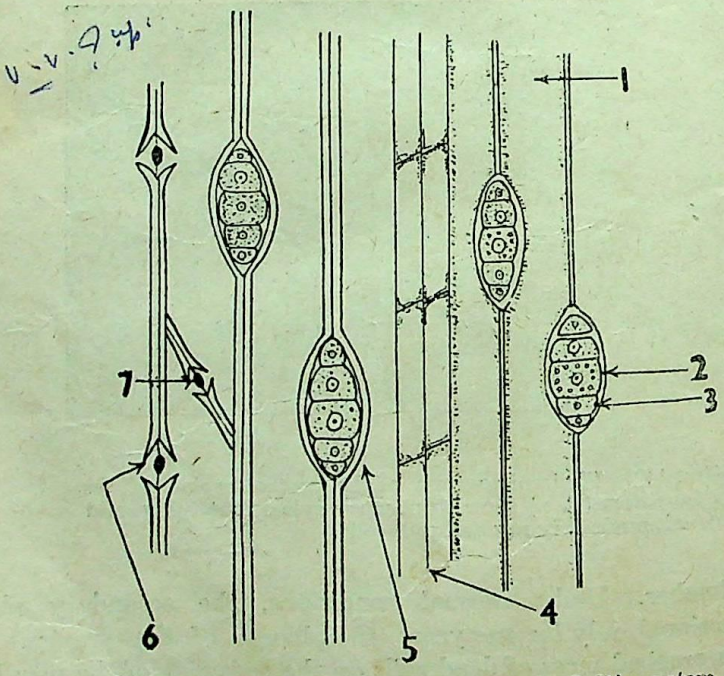

Fig. 144. Tangential longitudinal section of *Pinus* stem 1, Sieve tube ; 2, Starch cell ; 3, Albumen cell ; 4, Cambium ; 5, Med. ray showing parenchymatous cells ; 6, Bordered pit ; 7, Torus.

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and are usually less than a dozen cells in height. In the region of secondary phloem, the medullary ray consists of usual rectangular medullary ray cells containing **starch** and somewhat elongated **albuminous cells** containing a store of proteinaceous matter. In the region of secondary xylem, besides the usual starch cells, there are present certain radially elongated thick-walled cells with simple pits in their walls. These are the **tracheidal cells** and help in the radial diffusion of the sap. The structure of the meduallary ray can best be studied by cutting a number of tangential and radial longitudinal sections (Fig. 144).

By the time the vascular-cambium becomes active in the stele, there arises a continuous ring of meristematic cells, the **cork-cambium**, just

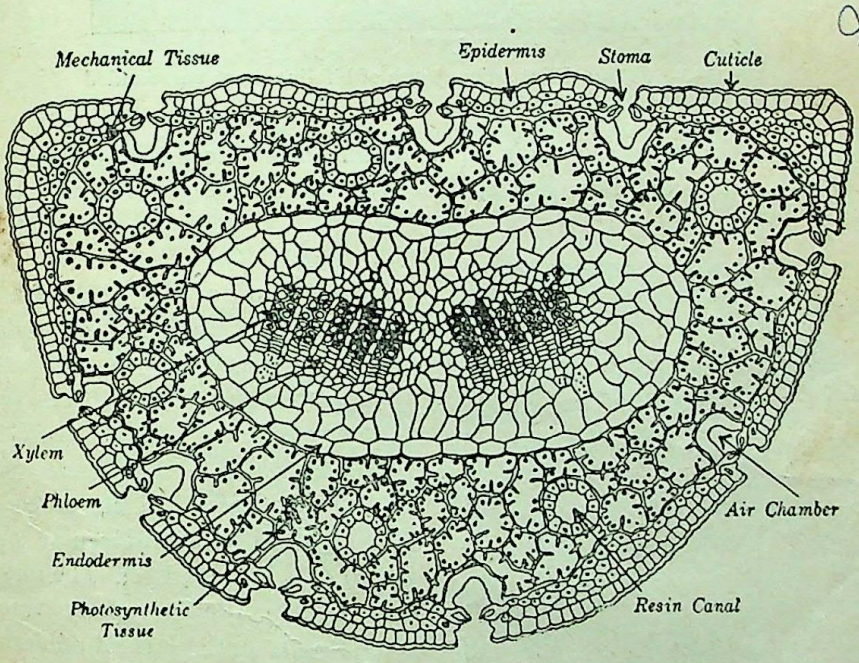

Fig. 145. T.s. of fine needle from a bifoliar shoot of *Pinus*.

beneath the epidermis in the cortical region. This cuts off **cork** on the outside and secondary parenchymatous cells towards the inner side. The cork is impervious to water and serves as **bark** to protect the stem from external injury and dessication.

The resin canals form a connected system throughout the cortex, xylem and phloem. They also run horizontally along many of the

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medullary rays. Each canal is bounded by glandular epithelial cells,

FIG. 146–A. *Pinus* Photomicrograph of bifoliar shoot surrounded with membranous sheaths.

which secrete **turpentine**. This serves as an antiseptic healing agent on a wound as it is oxidised, on exposure, to solid covering of resin.

FIG. 146–B. Photomicrograph of a portion of Pine needle.

Leaf. The pine-needle is a foliage-leaf of a highly specialized type (**xeromorphic**) peculiarly adapted by its structure to withstand adverse xerophytic conditions such as low temperature and a deficient water supply. A transverse section of the leaf of a 'two-needle' pine displays a semi-circular outline (Fig. 145, 146, 147). The outermost layer is the extremely thickened, highly cuticularised **epidermis** with a number of depressions. Each minute depression marks the **sunken** position of the **stoma** between two guard cells. Beneath this is the sclerenchymatous **hypodermis** which gets interrupted due to sub-stomatal air chambers of the sunken stomata. The underlying **mesophyll** shows no differentiation into **palisade** and **spongy** parenchyma. It consists of thin-walled chlorenchymatous cells with numerous plate-like infoldings from the wall which project into the cell cavities. These folds run in a circular manner round the cell and represent rigid, non-

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growing, ring-like zones in the wall. The presence of this peculiar structure, compensates for the reduction of the leaf-surface by increas-

FIG. 147–A. *Pinus* Photomicrographs of Trifoliar shoot.

ing the surface area of the individual cells. In the outer mesophyll,

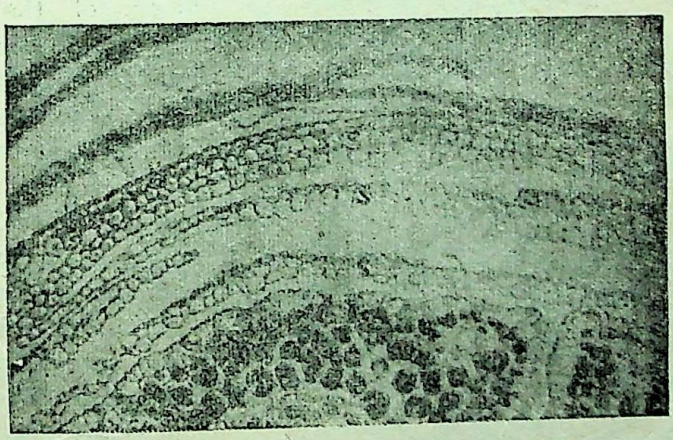

FIG. 147–B. Photomicrograph of a peripheral portion of a trifolior dwarf-shoot showing Sheaths (S) which cover the three needles.

lying below the hypodermis, are seen a number of **resin-canals** similar in structure to those of the stem.

The central region is bounded by a conspicuous **endodermis**, within which lies a many-layered **pericycle** in which two conjoint, collateral and parallel **vascular bundles** are arranged. The xylem of each bundle lies towards the upper flat surface of the leaf and the phloem towards the convex lower surface. The bundles remain unbranched from base to

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apex. Between the bundles are thin-walled parenchymatous

Fig. 147–C. Photomicrograph of the Stele of the *Pinus* needle.

cells. The pericycle, besides the thin-walled parenchymatous cells contains firstly, certain cells rich in proteins lying near the phloem of the vascular bundles. These are called **albuminous cells**, and help in the translocation of the food material from the mesophyll to the phloem. Secondly, there are present certain tracheid like lignified cells with bordered pits and without any living contents called **tracheidal cells**. They help to transfer the inorganic solutions from the xylem to the mesophyll. These two peculiar types of cells collectively form the **transfusion tissue** which helps in diffusion of nutritive solutions to and from the mesophyll and also makes up for the poor development of vascular bundles in the leaf. Thus the leaf shows prominent **xerophytic** character *e. g.*, needle-like form, thick cuticle, sunken stomata, strong sclerenchymatous hypodermis, simple vascular system and transfusion tissue.

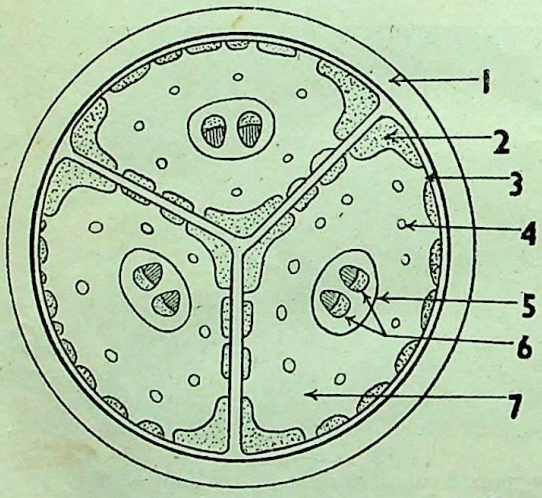

Fig. 148. *Pinus* Diagrammatic T. s. of trifoliar shoot 1, Sheath ; 2, Sclerenchymatous hypodermis ; 3, Sunken stoma ; 4, Resin canal ; 5, Endodermis ; 6, Vascular bundles ; 7, Mesophyll.

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Reproduction. It takes place by **spores** which are developed in **sporangia** and are borne on **sporophylls** which are aggregated to form compact **cones**. These structures though primarily asexual (diploid) are very well known as male and female cones because they are monospor-

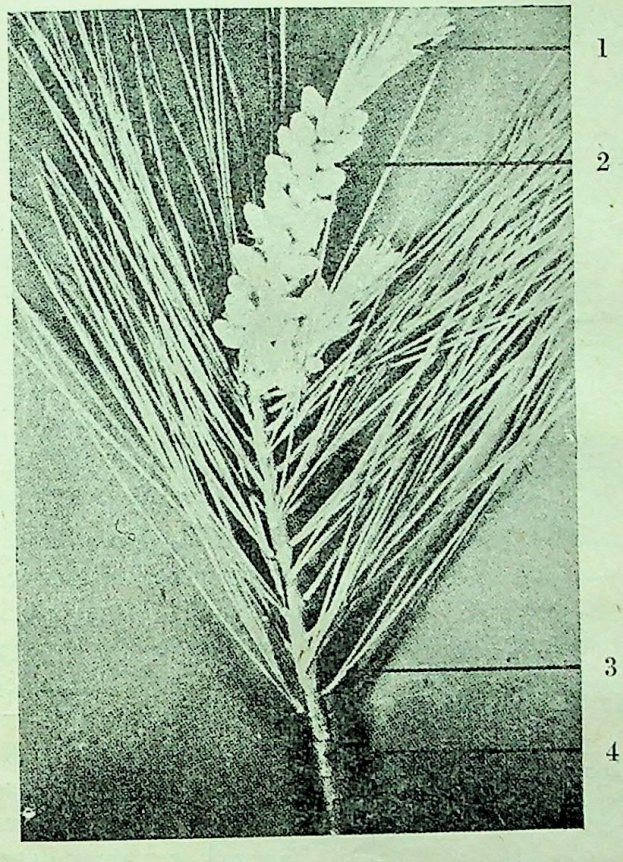

FIG. 149. Shoot of *Pinus* with a cluster of male cones. 1. Young dwarf shoots ; 2, Male cones; 3, Mature dwarf-shoot ; 4, Stem.

angiate in nature and both are borne on the same plant. *Pinus*, therefore, is **monoecious**. But bisporangiate strobili occur in certain species as anomalies as has been reported by Rao (1931) in *P. roxburghii*, Stell (1918) in *P. montana*, and Goebel in *P. marttima*.

Male Cones. These appear in May and are developed in clusters at the base of the youngest shoots in place of 'spur or foliar shoots'

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(Fig. 149) Each arises in the axil of a scale leaf at the base of the developing shoot of the current year and is comparatively small, rarely more than half an inch in length. It consists of a central axis about 5 mm. long, which bears 60-100 spirally arranged scaly **microsporophylls.** (Fig. 150). Each microsporophyll on its underside possesses two ovoid **microsporangia** or pollen sacs. The microsporangia are **eusporangiate** in development. The sporangial wall is about 4 layers of cells thick. Konar and Ramchandani (1959) in case of *P. wallichiana* have reported that the sporangial wall consists of an outer epidermis, two middle layers and a glandular tapetum. The microsporangium, when young, possesses a perepheral **tapetum** and a central **archesporial tissue** which produces many diploid **microspore mother cells**, each of which divides meiotically to develop four haploid **microspores** or pollen grains. Sethi (1928) reports that the meiotic process in *P. roxburghi* takes places somewhere in the last week of January ; whereas Bold (1957) reports, in *P. virgianana,* to be of annual recurrence between March 15 and April 1. The haploid number (n) of chromosomes in all species of *Pinus* is twelve.

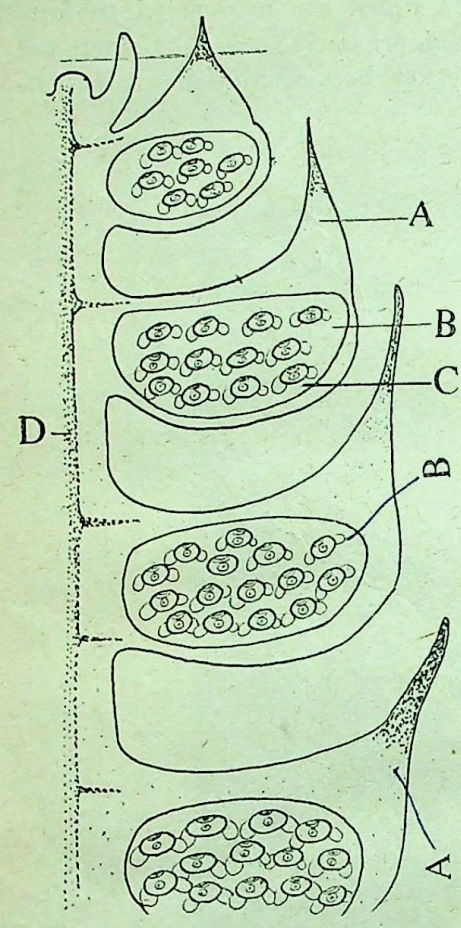

FIG. 150. L. s. of male cone of *Pinus* (diagrammatic) (A, Microsprophyll; B, Microsporangium; C, winged pollen grains ; D, Axis of cone).

The Microspore and development of Male-gametophyte. The microspore has got a three-layered wall. The **extine** or the outer layer is heavily cuticularized and is seen only on one side of the spore. It does not cover the spore completely. The middle-layer or **exo-intine** covers the spore completely forming two conspicuous balloon-like expansions on either side containing air. This makes the microspore more buoyant thus justifying its anemophilous nature. The **intine** or the inner layer is very thin and delicate (Fig. 151).

At first, the microspore is a unicellular body. When mature, they do not leave the sporangium in this condition but germinate *in situ.*

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The germination is marked by the division of the spore into a very small flattened **prothallial cell** and a large **tube cell.**

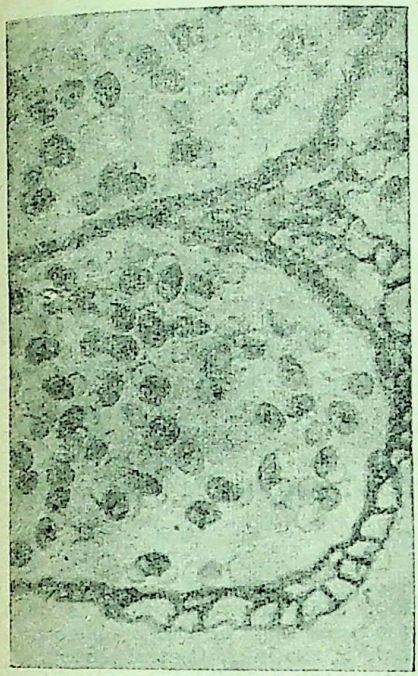

Fig. 151. Photomicrograph of pollen sac of *Pinus* (L. s.) showing winged pollen grains.

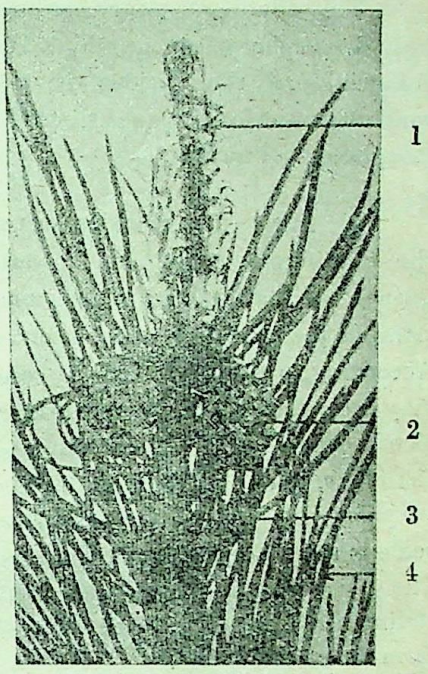

Fig. 152. Terminal portion of branches of *Pinus* with young female cones; *1*, Young dwarf shoot; *2*, Female cone; *3*, Stem; *4*, needles.

At this stage dehiscence of the microsporangium takes place by a longitudinal fissure along a region of thin-walled cells exposing the spores to the mercy of the wind. They ultimately become empty so that the cone rapidly withers off and falls down.

Female Cones. These develop laterally in clusters from one to four in the axil of scale-leaves in place of branches of unlimited growth (Fig. 152). Uusually, these develop in winter somewhere during January, February and eventually grow much larger than the male-cones, ultimately becoming ready for pollen reception in the next spring. When young, each is small, erect, of reddish colour consisting of a **central axis** bearing spirally arranged scale-like outgrowths. These are made up of two kinds of structures. Firstly, the outer smaller leathery **bract-scales** developed directly on the axis and secondly larger, woody **ovuliferous scales** developed from

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the former (Fig. 153). Each ovuliferous-scale bears two ovules on its upper surface.

This double structure has long been a morphological puzzle. The following are the various theories which account for its much disputed morphological nature.

1. **Sachs and Eichler** regard the ovuliferous scale as an outgrowth of the bract scale comparable to the **ligule** or placenta. According to them the female cone may be regarded as a **female flower.** The cone-axis is the elongated thalamus, the bract-scale is the carpillary scale, the ovuliferous scale is the placenta bearing ovules. The gynoecium is apocarpous with rudimentary carpels which do not form a closed ovary.

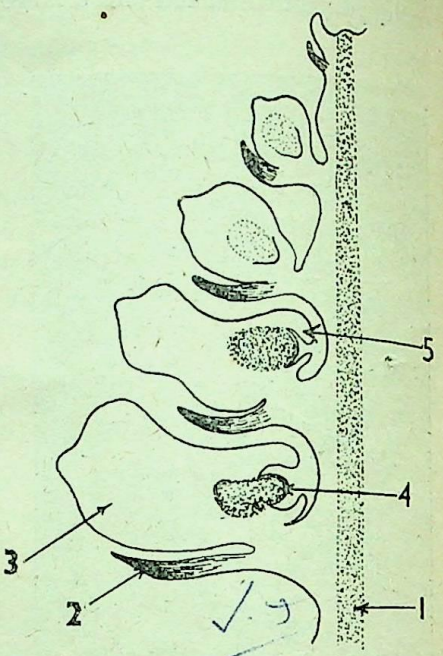

FIG. 153. Diagrammatic L. s. of the female cone of *Pinus* only one half is shown *1*, Central axis ; *2*, Bract scale ; *3*, Ovuliferous scale ; *4*, Ovule ; *5*, Integument.

2. **Kubart and Bessey** regard the ovuliferous scale as a combined outgrowth of the ovules and may be called an **aril** or an enlargement of the *chalaza* of the ovules.

3. **Delpino** regards the ovuliferous-scale to be formed from two lateral lobes of **bract scale** which have been turned inwards and fused together.

4. **Hirmer** regards the ovuliferous scale and bract scale as parts of one structure, which has forked vertically as the sporophylls in *Cheirostrobus.*

5. **Braun** regards the ovuliferous scale to represent the first two leaves of an **axillary shoot**, which are fused by their adaxial margins.

6. **Florin** regards the female cone as an **inflorescence.** According to him the cone-axis is the peduncle axis, each bract scale as a true bract in the axil of which is a short modified reproductive shoot ; the ovuliferous scale bearing a rudimentary female flower.

Ovules. Each ovule arises as a group of cells forming a rounded hump of tissue—the **nucellus**, on the upper surface of the ovuliferous scale. Soon

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a two-lipped covering layer—the **integument** surrounds the nucellus except the inner end where a wide **micropyle**—an aperture is left. The integument is fused to the nucellus except for a short distance near the micropyle. It shows three layers outer and inner fleshy layers and the middle being stony (Fig. 156). The micropyle is directed obliquely towards the cone axis. At the apex of the nucellus a **hypodermal cell** enlarges to form a large **archesporial cell**. This divides to form a **tapetal cell** and a **megaspore-mother-cell**. The latter divides meiotically to form a linear tetrad of four haploid megaspores (Fig. 154E). Out of these, three apical ones (near the micropyle) degenerate, the last *i. e.*, farthest from the micropyle matures and is called the **functioning megaspore** or **embryo-sac.** It is at this stage that the ovules are pollinated. Thus, the pollination takes place when the megaspores have been formed in the ovule. The development of embryo-sac takes place only after pollination (Fig. 154R).

Pollination. This involves the transfer of **anemophilous** microspores or pollen grains to the ovule and is facilitated by the balloon-like expansions. Usually the pollination occurs somewhere about the end of May in North temperate regions. At this time the central axis of the female cone elongates separating the ovuliferous scales, which upto this time have been closely pressed together. By this time, yellow clouds of microspores are already in the atmosphere. Most of the pollen is wasted, but some of the pollen grains are blown by wind in between the ovuliferous scales and are finally lodged in the micropyle. The nucellus secretes a **mucilaginous fluid** which oozes out from the micropyle. This entangles the pollen grains and as it dries up, they are finally brought to rest on the apex of the nucellus. The growth in thickness of the apical portion of the integument seals the micropyle and imprisons the pollen grains permanently (Fig. 154R).

Further Development of Male Gametophyte. The pollen grain resumes germination on the surface of the nucellus. Now the tube cell divides forming a **second prothallial cell** at the top of the first one formed before (Fig. 155D), pollination. Both the prothallial cells soon disorganise. The remaining cell divides to form a rounded **antheridial** (Generative) **cell** at the top of the disorganising prothallial cells and the tube nucleus. At this, the exo-intine of the microspore breaks between the two balloon-shaped expansions so that the delicate intine comes out in the form of a short **pollen-tube** (Fig. 155). This grows slowly in the nucellar tissue and rests throughout the winter. In the next April, the antheridial (generative) cell divide into a **stalk** and **body cell.** The latter divides to form two **male cells** (Fig. 155G) The stalk cell and the body cell get detached from the microspore wall and migrate through the pollen tube. Ultimately the mature male gametophyte contains only 2 male nuclei in the elongated pollen tube, the rest being all degenerated. At this stage the mature male gametophyte awaits fertilization.

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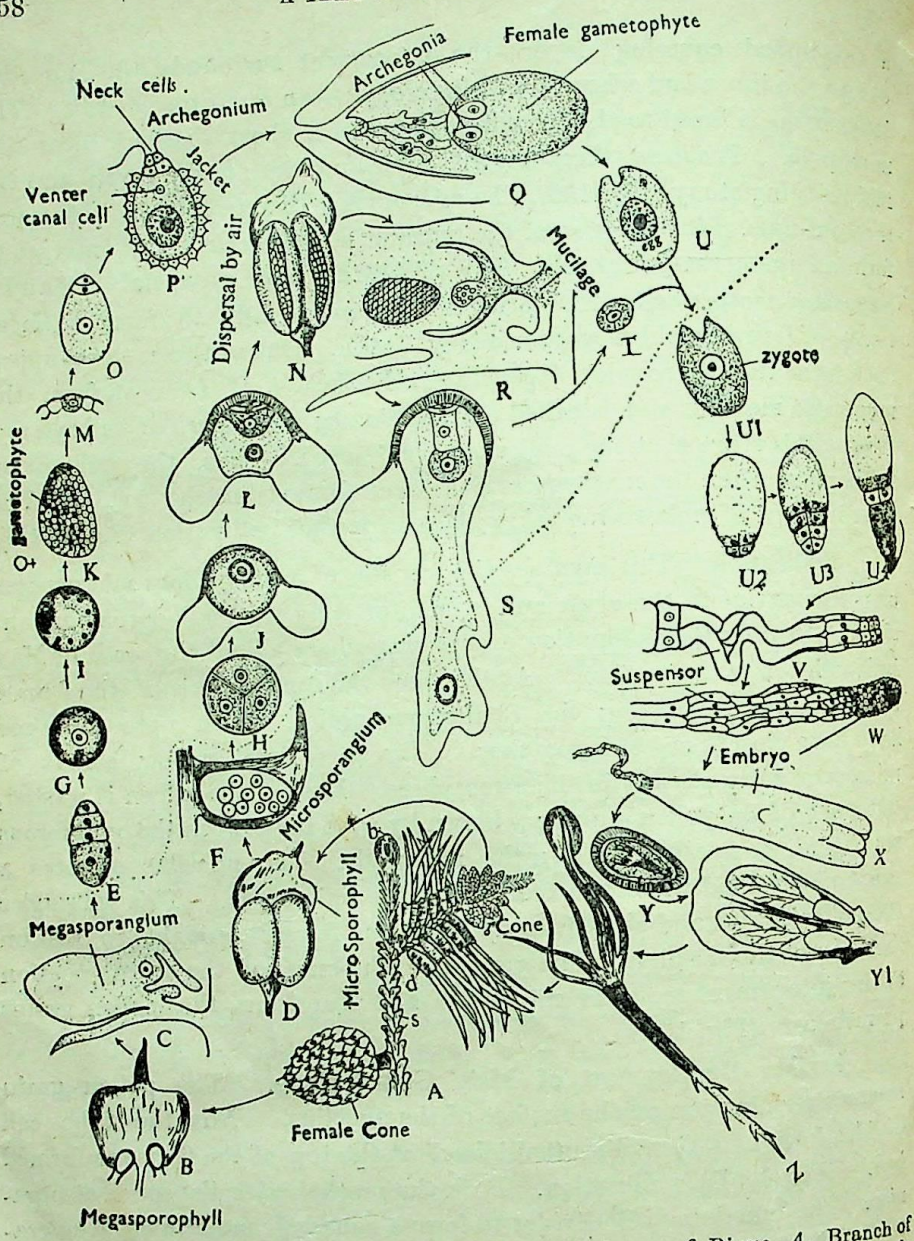

FIG. 154. Diagrammatic representation of the life history of *Pinus*. *A*, Branch of Pinus tree with a terminal bud (b) dwarf short (c) which arise in the axil of scale leaves (*s*) ; *B*, Megasporophyll with 2 ovules ; *C*, An ovule with ovuliferous scale showing megaspore mother cells (2x) ; *D*, Microsporophyll & microsporangia ; *E*, Linear tetrad of 4 megaspores only the basal one is functional ; *F*, Pollem mother cells in pollen sac ; *G*, Megaspore mother cell (2x) ; *H*, Tetrad of 4 microspores (x) ; *I*, Free-nuclear division of megaspore nucleus ; *J*, A young microspore ; *K*, Female gametophyte ; *L*, Pollination stage of the winged pollen grain (3 celled stage) ; *M*, Archegonial initial ; *N*, A microsporophyll showing ruptured pollen sacs liberating the winged pollengrains ; *O—P*, Development of archegonia ; *Q*, An ovule showing fertilization. Pollen tubes are soon in the nucellus and archegonia in the female gametophytic tissue ; *R*, Pollination stage, showing exudation of mucilage from the micropyle. Pollen grains are seen in the pollen chamber ; *S*, Pollen grain showing a well developed pollen tube, two prothallial cells, a body and a stalk cell ; *T*, Male cell (x) *U*, egg (x) ; *V*, Zygote (2x) ; *u—w*, Development of embryo ; *X*, Mature embryo ; It seed ; *Y*1, winged seed attached to the megasporophyll ; *Z*, Germinating seed with a young sporophytic plant.

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Development of Female Gametophyte. After pollination, the female cone becomes green and increases in size. The megaspore or embryosac

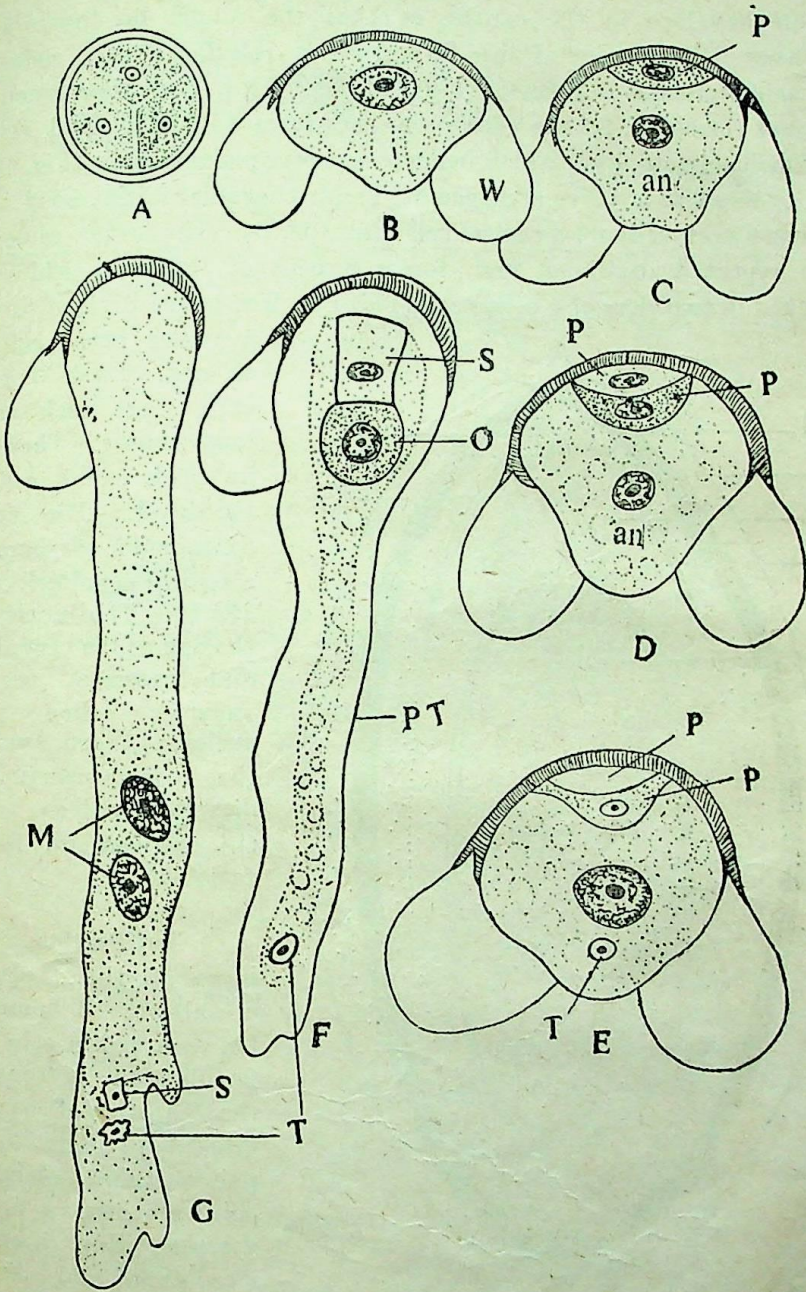

FIG. 155. Microspore and development of Male Gameto phyte of *Pinus*. *A*, Tetrad of spores ; *B*, A microspore with two wing-like expansions ; *C*, Division of microspore into a small first prothallial cell (*P*) and a large antheridial cell (an) ; *D*, Development of second prothallial cell (P') ; *E*, Later stage showing the disappearance of first proth. cell and production of a tube nucleus (T) ; *F*, Disappearance of prothallial cells. The anth. cell divides to form a stalk cell (s) and a body cell (o) and the pollen tube (Pt) develops ; *G*, Mature male gametophyte showing the division of Body cell into two male cells ; (M) Stalk cell and tube nucleus are degenerating.

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undergoes free-nuclear division developing about 2000 nuclei. A large vacuole develops in the centre, so that the nuclei lie towards the periphery. By centripetal wall formation, a cellular tissue, **endosperm** or **female prothallus** is formed (Fig. 154, K). This is neither green nor possesses rhizoids. At the micropylar end, from the superficial cells of the female gametophyte which behave as **archegonial initials** (Fig. 154M) and develop two or three **archegonia**. The archegonial initial divides into a **primary neck cell** and a **central cell** (Fig. 154, O). The former undergoes three repeated divisions and forms 8 cells of the neck which are arranged in two tiers of 4 cells each (154, P). The latter divides to form a **venter canal cell** and an **egg**. Each consists of a short **neck** and a large venter. There are no neck canal cells in the neck. The venter contains an **oosphere** and a **ventral canal cell** (Fig. 154 P). The nucleus of the egg cell is very large and possesses peculiar vacuoles called **paranuclei**. When mature the ventral-canal cell disorganises so that the egg awaits fertilization.

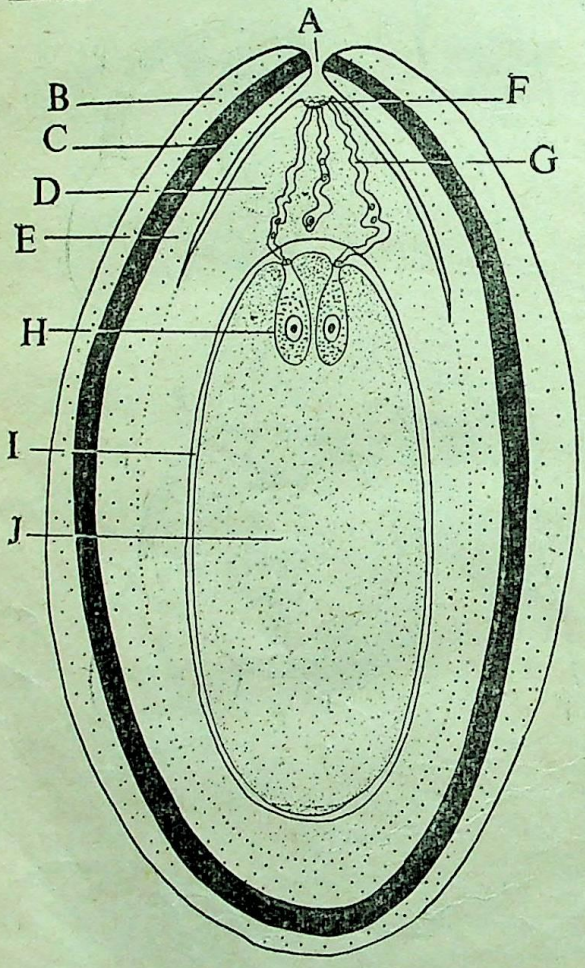

FIG. 156. L. s. of Mature ovule of *Pinus* showing fertilization. *A*, Micropyle ; *B*, Outer fleshy layer ; *C*, Middle stony layer ; *D*, Nucellar tissue ; *E*, Inner fleshy layer ; *F*, Germinating pollen grains in the pollen chamber . *G*, Pollen tube ; *H*, An archegonium ; *I*, Megaspore membrane ; *J*, Female gametophyte.

Fertilization. The lapse of time, usually of about 13 months, between pollination and fertilization is one of the features of special interest in *Pinus* The pollen tube elongates till it reaches an archegonium. Here it enters its neck and bursts often throwing out short branches. The two male nuclei enter the venter but only one fuses, the other dies away. The fusion of the male nucleus with the egg intitutes fertilization, developing a thick-

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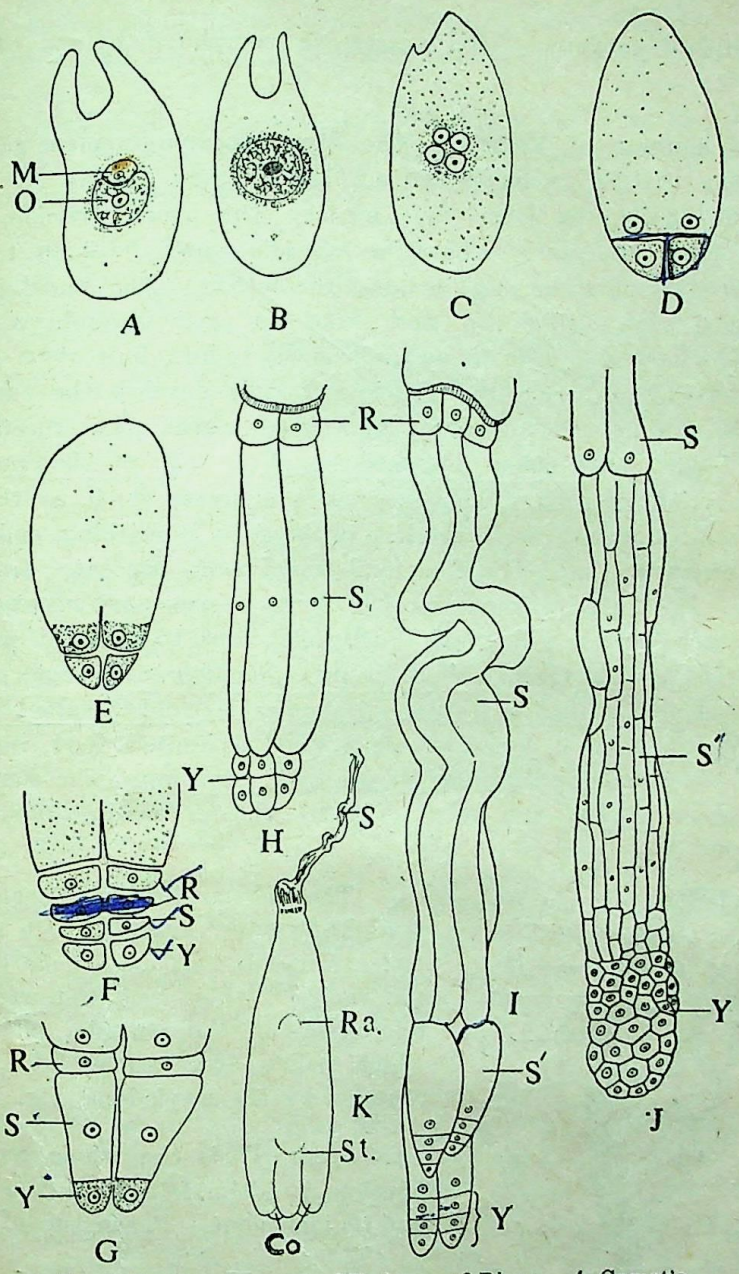

FIG. 157. Development of Embryo of *Pinus*. *A*, Gametic union of a male nucleus (M) with the egg nucleus (O) *B*, Zygote (2x); *C*, Division of diploid zygotic nucleus into 4 diploid nuclei; *D*, Four nuclei sink to the base of the oospore; *E*, Division of the nuclei to form two rows of 4 cells each; *F*, Four rows of four cells each—later stage (two of each row shown); *G*, Suspensor cells (S) elongated; *H*, later stage showing Rossette cells (R) Suspensor (S) Embryonal cell (Y); I, Initiation of 4 embryos by the separation of the four rows of embryonal cells and development of secondary suspensors (S'); *J*, Mature stage showing only one functional embryo and elongated secondary suspensors (S'); *K*, Mature embryo showing shrivelled suspensor (S) an embryonic axis differentiated into Radicle (Ra), Stem tip (St) and Cotyledons (Co).

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walled diploid oospore. This process is completed by end of June (Fig. 156).

Development of Embryo. The diploid oospore nucleus moves towards the bottom or basal end of the oospore. Here it divides twice mitotically to form four nuclei. One more division brings their number to eight. Cell walls are laid down between the four basal nuclei forming four small cells at the bottom. The remaining four free nuclei soon disorganise and take no part in embryo formation. The four small cells divide transversely to form four rows of cells each consisting of three cells. The lowest cells develop the **embryonal** cells, the middle cells **suspensor** and upper ones the **rosette** cells (Fig. 157 F). This peculiar differentiation of the cells of the proembryo is characteristic of *Pinus*. The suspensors elongate much so that the embryonal cells are thrust down deep in the food nourishing endosperm or female prothallus. The four embryonal cells separate from one another. Each divides transversely to form a **secondary suspensor cell** and **embryonal proper cell** which finally develops to form a **potential embryo** (1571). Thus from a single oospore four potential embryos are formed. This is a peculiar feature of coniferales and is called **clevage polyembryony**. But in course of time, due to limited food, only one survives the remaining three degenerate after starving. The suspensors finally shrivell away and take no part, whatsoever, in the embryo formation.

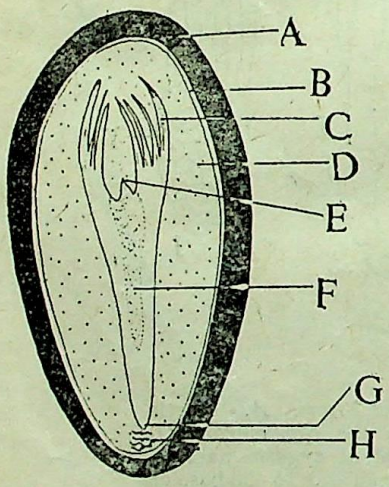

Fig. 158. L. s. of seed of *Pinus*. *A*, Seed coat; *B*, Perisperm; *C*, Cotyledons; *D*, Endosperm; E, Stem tip; *F*, Hypocotyl; *G*, Radicle; *H*, Remains of suspensor.

The embryo elongates developing a straight structure in the centre of the endosperm. It consists of a short axis—the **radicle** which points towards the micropyle and the **plumule** (stem tip) which points downwards and is surrounded by the cotyledons (Fig. 157 K).

Seed. It is the whole structure developed ultimately from the ovule and its inclusions. It consists of:

1. **Embryo.** This is the newly developed young sporophyte differentiated into Radicle, Plumule and Cotyledons and lies in the centre of food laden endosperm.

2. **Endosperm.** It is a nutritive tissue whose cells are filled with reserve food for the embryo. This tissue is the only persisting tissue of the female gametophyte.

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3. **Perisperm.** It is the persisting sporophytic nucellar tissue which helps in providing nutrition to the female gametophyte and embryo.

4. **Seed Coat.** It is formed only from the middle stony layer of integument. The outer and inner soft layers disorganise. Thus the seed coat is a hard stony layer.

5. **Wing.** A membranous wing develops as a result of the separation of the upper surface of the ovuliferous scale. This helps in dispersal of seeds by wind to long distances.

Thus the seed consists of structures belonging to two generations *i. e.*, the gametophytic and sporophytic. The endosperm belongs to the former and the embryo, perisperm and seed coat to the latter (Fig. 158).

FIG. 159. Mature female cones in the third year opening to liberate the winged seeds of *Pinus*.

Dispersal of Seeds. In the third year, the female cone matures becoming brown, woody and dry. When seeds are mature, under dry conditions only the cone-axis elongates so that the ovuliferous scales gape apart explosively. Each scale has got a pair of winged seeds. These are liberated from the cones and are blown away by the wind to long distances (Fig. 159).

Germination of Seed. The seeds may germinate in the spring or may remain dormant if conditions are not favourable. Under suitable conditions, the seed absorbs moisture which causes the splitting of the seed coat. The radicle grows down towards the soil, while the plumule grows upwards towards the light spreading apart the green cotyledons. They may become green while still enclosed within the seed coat. This is done at the expense of the endosperm. The radicle develops into a primary tap-root while the plumule develops into a primary axis (shoot) of unlimited growth on which are borne acicular green leaves spirally (Fig. 154, Z). The seed shows **epigeal** germination, in that the cotyledons carry the seed up along with them. This condition better known as **'juvenile condition'** persists until the seedling is 3 or 4 inches high. The leaves become smaller till they become mere scale-leaves bearing dwarf shoots in their axils. This condition is a primitive feature characteristic

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of Pines. Ultimately from this mesophytic **'juvenile'** form there develops a xerophytic **'adult'** plant.

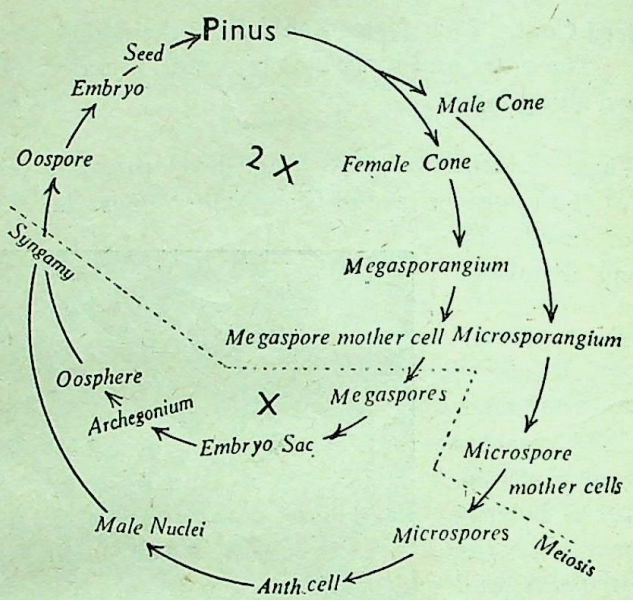

FIG. 160. Life-cycle of *Pinus*.

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CHAPTER 14

GNETALES

The Gnetales are not able among gymnosperms for the presence of certain angiospermous features such as : the occurrence of **true vessels** in the secondary wood ; **covering of the ovule**, besides the true integument, considered to be the equivalent of ovary wall ; the presence of **'perianth'** ; and the occurrence of organs consisting of a short axis of stalk bearing a terminal group of more or less united miscrosporangia containing microspores, considered to be equivalent to **stamens**. In the light of these features, the Gnetales have been regarded as a transition group between the gymnosperms and the angiosperms. Since the pollination is still an ovulur function, and that no true style or stigma is present, the Gnetales justify their inclusion in gymnosperms.

This order includes three genera *Ephedra*, *Welwitschia*, and *Gnetum*. These differ remarkably in habit and distribution which suggest the existence of older and more widely distributed forms of a formerly larger and more united order. Their fossil records, however due to their xerophytic habitat are remarkably few and do not go beyond the tertiary period, so that we have little idea about their ancestry. Their ungynmosperm like habit suggests that they are probably of fairly recent appearance.

The following are the only common characters of this heterogenous group which keep the three genera together :

(a) True vessels in secondary wood.
(b) Compound strobili (both staminate and ovulate) resembling inflorescences.
(c) Long micropylar tubes formed by the prolongation of the apex of inner integument.
(d) Opposite leaves.
(e) Dicotyledonous embryo.
(f) Absence of resin canals.

For a long time these three genera had long been considered to constitute a single, family Gnetaceae. But on account of a lot of criticism by a number of workers on the heterogeneity of this order,

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Markgraf (1926) splitted it into three distinct families—Ephedraceae, Welwitschiaceae, and Gnetaceae each with a single genus. In the light of such striking divergence between the three genera, such as the **haplocheilic** type of stomata of *Ephedra* (resembling to those of Cycadales, Ginkgoales and Coniferales) and the **syndetocheilic** type revealed by *Welwitschia* and *Gnetum* (resembling angiosperms) and the **appendicular** (not *cauline*) position of ovule of *Ephedra* led Florin (1931), Eames (1952) and Bold (1957) to segregate the old order of Gnetales into three distinct orders : Ephedrales, Welwitschiales and Gnetales.

We have taken *Gnetum* the highest evolved gymnosperm as the repsesentative of new order of Gnetales because it deserves mention on account of close similarities with angiosperms.

GNETUM

Systematic position

Division—*Tracheophyta*
Sub-Division—*Pteropsida*
Class—*Gymnospermae*
Order—*Gnetales*
Family—*Gnetaceae*
Genus—*Gnetum*

Geographical distribution. *Gnetum* (Malaya—*gnenom*), a genus of evergreen trees, climbing shrubs or lianas is distributed in tropical regions of Africa, Asia and South America. Out of 34 species, most of them when not in fruit, might be mistaken for dicotyledonous plants. About 19 species are confined to tropical Asia, and the islands between Australia and Asia, whereas 12 species grow in South America and are restricted in distribution to the northern coast, Brazil, Ecuador and West Indies. No species have so far been reported from North America, Australia or Europe. In India only five species are met with as follows :—

1. **G. gnemon**—an evergreen shrub or a middle-sized tree with narrow conical crown and rather short drooping branches distributed in Assam, Khasi and Jayanti Hills and hills of Manipur. Trunk grey marked with conspicuous or faint leaf scars, leaves broadly elliptic and accuminate.

2. **G. latifolium**—a large evergreen climber distributed from Andamans and Nicobar Islands through Malaya to Phillipines leaves variable in shape and size.

3. **G. montanum**—a large woody climber with dark grey bark peeling off in pieces found in tropical Himalayas, from Sikkim eastwards Bengal, Assam, Khasi and Manipur Hills upto an height of 3000 feet above sea level. It is North Indian in distribution.

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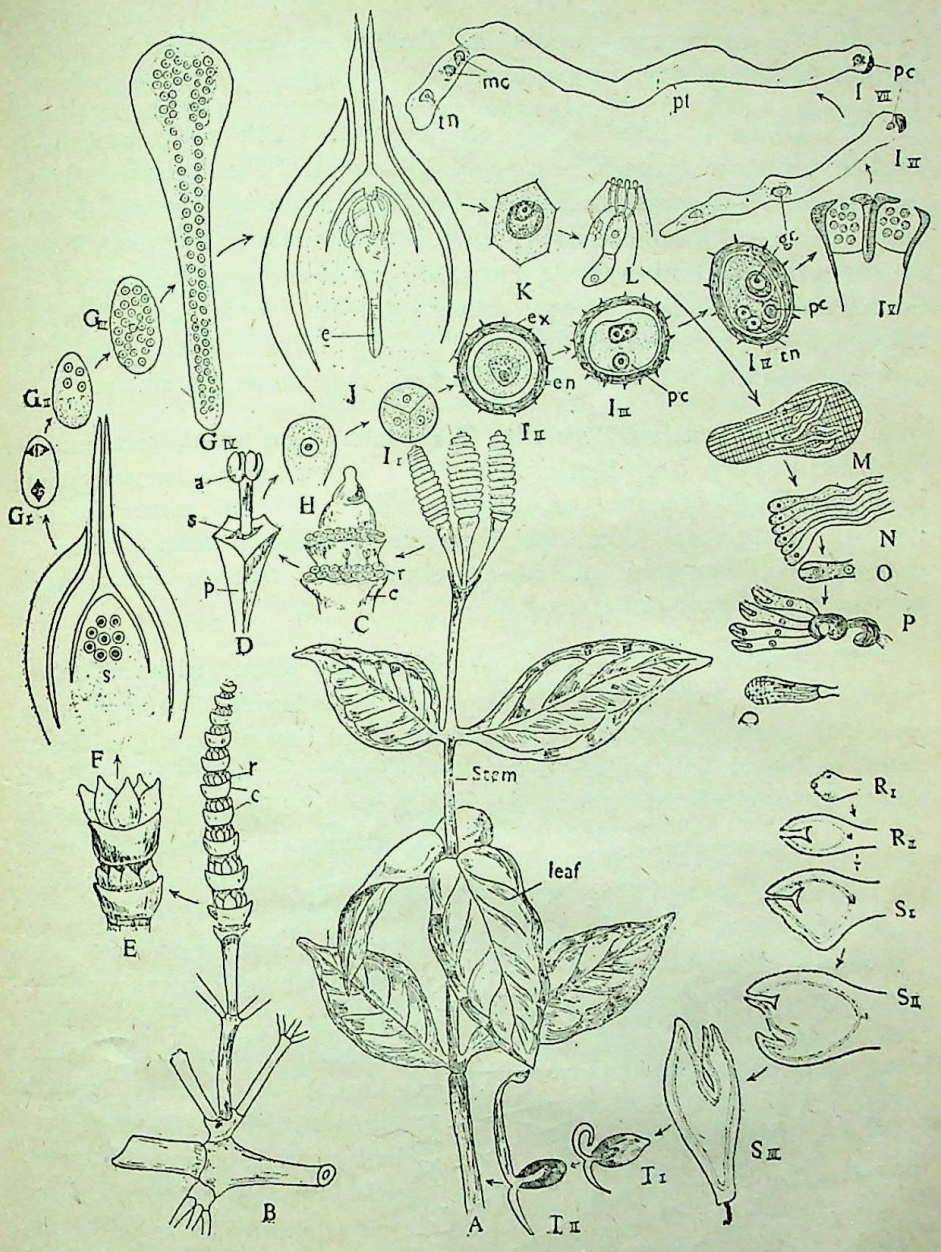

FIG. 161. Diagramatic representation of life-history of *Gnetum*. *A*, Branch of Gnetum showing habit and male cones arranged in a panicle ; *B*, A branch bearing female cones ; *C*, A panicle of male flowers ; *D*, A single male flower having a stalk and two unilocular anthers ; *E*, A portion of panicle of female flowers. Note a single ring of female flowers above each collar ; *F*, An ovule showing megaspore mother cells ; *Gi*, *Gii—Giv* Development of female gametophyte ; *H*, Microspore mother cell in meiosis ; *I—ii*, Microspore ; *I—ii iii* Development of an anther II Tetrad of microspores ; *I—ii*, Microspore ; *I—ii iii* Development of microspore till pollination stage (3 celled) I—L. S. of anther showing liberation of microspores ; *I vi—vii* Germination of microspore in the ovule and development of male nuclie ; *J*, L. s. of ovule at fertilization showing endosperm and pollen tubes ; *K*, Zygote ; *L*, Division of zygote into cells which develop primary suspensor tubes ; *M*, Endosperm containing suspensor tubes ; N, coiling of tubes , *O*, A suspensor tube with a "peculiar cell". , *P*, Shedding stage of seed . *Q*, Embryonal mass developed at the tip of suspensor tube , *Ri.—ii*, Development of embryo . *Si—Siii*, Development of "feeder" , *Ti*, *Tii*, Germination of seed and development of young sporophyte , *r*, Ring of flowers , *c*, Collar (cupules) , *s*, Spore mother cell , *p*, Perianth , *s*, Slit, *a*, anther, *e*, Endosperm, *ex*, Exospore, *en*, Endospore , *pc*, Prothallial cell , *gc*, Generative cell , *tn*, tube nucleus , *mc*, Male cells , *pt*, Pollen tube)

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4. **G. contractum**—occurs in Travancore and Nilgiris at an altitude of 5000 feet above sea level.

5 **G. ula**—a large woody climber with thick scaly bark and swollen joints reaching the tops of tall trees. The lower part of the stem is leafless whereas the leaves occur higher up near the branches of the tree to which the climber clings. Found in moist evergreen, forests of Western and Eastern Ghats upto 4500 feet above sea level especially in Khandala, Kanara, Poona, along Malabar coast, and Mysore; Nilgiris in Kerala; Chenath Nair and Pulney Hills Madras; Godawari district in Andhra; Orissa; Chota Nagpur; and South Andamans.

Habit and External Vegetative Characters. The plants are mostly climbers or very large **lianas** which twine or trail over other tall plants reaching a height of more than 100 feet. There are no leaves for the first 40 or 50 feet. Some of them are **tree-like** in habit such as *G. gnemon* and *G. costatum*. A few are **shrubs**. *G. trinerve* occurs as a **parasite** on large tropical trees.

The most striking feature is the **dicot-type leaves** with reticulate venation (Fig. 161 A). From the axile of the leaves of primary stem arise more than one axillary side **shoots**. These are differentiated into shoots of **limited** and **unlimited** growth. Usually in climbing forms, the foliage leaves are borne on branches or shoots of limited growth while there are some scale leaves on the branches of unlimited growth as well as on the main shoot. In some cases such as *G. scandens* the leaves are borne on both types of branches. Each branch of limited growth possesses about 9—10 leaves arranged in decussate pairs. Usually the pairs are often crowded and lie in one plane so that the branch of limited growth ('dwarf shoot") looks like a pinate leaf. The **leaves** are of variable shape and size on the same plant. Each **exstipulate** leaf has got a small stalk and is broadly oval in shape with an entire margin and acute apex. The leaf shows **unicostate reticulate venation,** on each side of the mid-rib there are five prominent large **lateral veins**. Some of the branches from the lateral

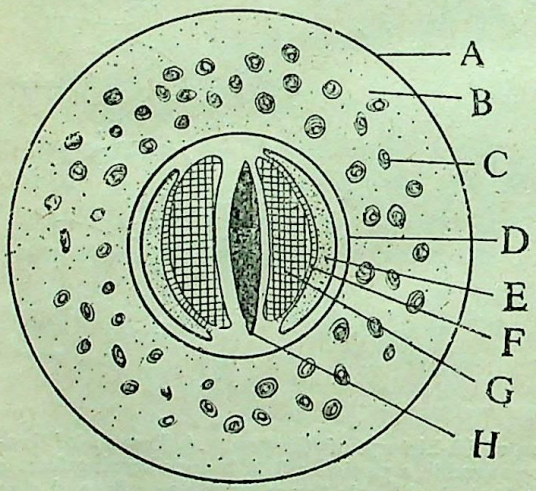

FIG. 162. Diagrammatic T. s. of *Gnetum* root showing a diarch structure. *A*, Epidermis; *B*, Cortex; *C*, Sclerids; *D*, Endodermis; E, Sec. phloem; *F*, Cambium; *G*, Sec. xylem; *H*, Protoxylem.

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veins form sub-marginal **loops**, from which are given off still finer branches at various angles and end blindly towards the margin. Such a peculir reticulate venation is characteristic of dicotyledonous angiosperms.

The **roots** are not very deep. The normal tap root persists only four years and is then replaced by adventitious roots.

Anatomical Structure

Root. The root shows a **diarch** structure. The simple parenchymatous **cortex** shows irregular distribution of fibrous elements. The outermost layer is the epidermis and it is here, in case of adult roots, where a **phellogen** arises, an abnormal feature for gymnosperms (Fig. 162).

The **stele** in young roots shows two radial bundles which are separated by a small parenchymatous region but the mature root reveals a single plate of xylem with only one row of tracheids with two exarch protoxylem points. The protoxylem consists of reticulately thickened tracheids. The **secondary growth** takes place in the normal manner. The secondary xylem consists of very large vessels and tracheids showing multiseriate bordered pits, some of which are metamorphosed into **vessels**. Here only the pit disentigrates to form a single perforation in the transverse septum. Such single perforation is characteristic of angiosperms. The **phloem** consists of sieve tubes and companion cells. These are peculiar and deserve mention as they originate from **separate cells** in two different layers of the cambium, unlike those of angiosperms which develop from the sub-division of single cells. Large **medullary-rays**, composed of parenchymatous cells impregnated with crystals of **calcium oxlate**, form a prominent feature of the root.

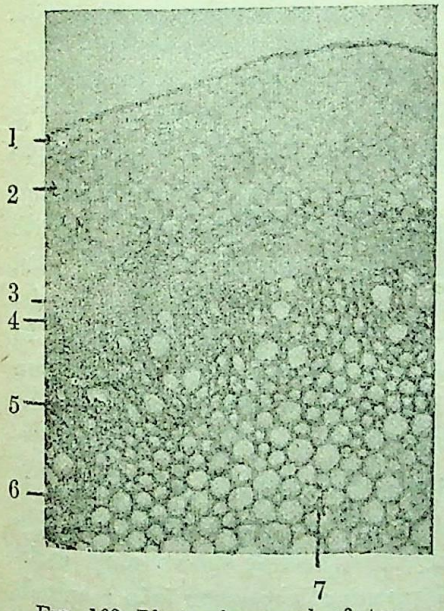

FIG. 163. Photomicrograph of stem of *G. gnemon* showing beginning of secondary growth. *1*, Epidermis; *2*, Cortex ; *3*, Sclerids ; *4*, Phloem ; *5*, Xylem; *6*, Thick-walled conjunctive tissue ; *7*, Pith.

Stem. A young stem in a transverse section reveals a ring of long conjoint, collateral, endarch bundles showing a **eustelic** structure (Figs. 163, 164). The medullary rays are large. The cortex is bounded by an

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outermost thick-walled epidermis with a number of stomata. Below the epidermis, lies a multicellular parenchymatous region in which sclerids and acicular spicular cells containing calcium oxlate crystals are irregularly distributed. The xylem is typically like that of root but the tracheids have mostly uniseriate ordered pits which are separated by conspicuous bars of sanio.

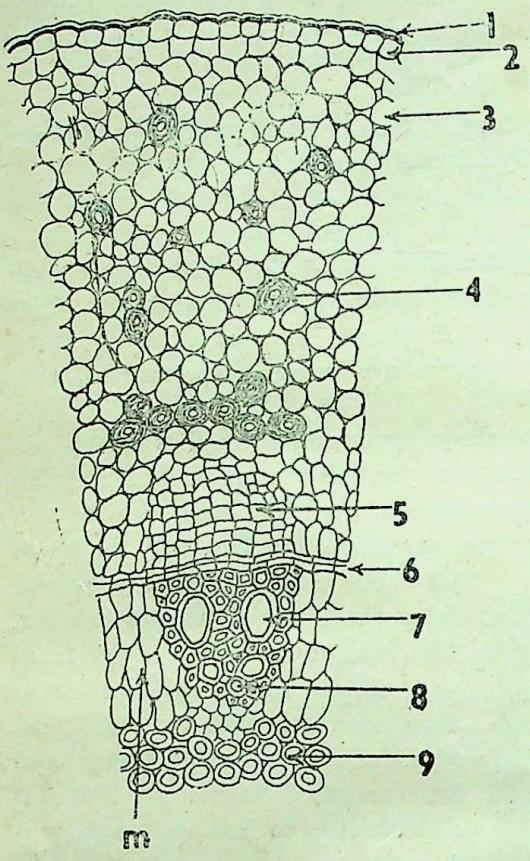

FIG. 164. A portion of T. s. showing detailed structure. *1*, Cuticle ; *2*, Epidermis ; *3*, Cortex ; *4*, Sclerids ; *5*, Phloem ; *6*, Cambial ring ; 7, Meta xylem ; *8*, Protoxylem ; *9*, Thick-walled conjunctive tissue. **M.** Medullary ray.

The secondary growth is abnormal in that after normal secondary growth has taken place, a fresh cambium arises in the phloem itself and this cambium forms another ring of xylem and phloem. Thus in *G. scandens* a large number of rings may be formed, but they have no relation with any seasonal changes and hence should not be mistaken for annual rings. In some cases bits of cambium arise in the inner cortex so that the extra stelar bundles may be formed.

The **corkcambium** arises in the epidermal region but its activity is **not uniform** throughout the ring, so that in mature stems only one side may show a broad zone of cork while the otherside shows olny cork-cambium cells dividing. This **differential growth** of phellogen is in response to the climbing habit of the plant. The side which lies towards the supporting stem has very little cork while the other which is exposed to the atmosphere develop thick zone of cork.

The **pith** is very well differentiated into a peripheral sclerenchymatous and a central parenchymatous region. The latter shows a deposit of calcium oxlate.

Leaf. The leaf is bounded by upper and lower **epidermis**. The lower epidermis contains dictoyledonous type stomata. The **mesophyll** is differentiated into a single-layered **palisade** and **spongy tissue**. Besides

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Besides these, are present some **spicular cells,** like those of stem, and **latex tubes**. The **vascular strands** are conjoint, collateral and endarch. Each vascular bundle is surrounded by sclerids on all sides. These sclerids are also present in isolated patches throughout the mesophyll and two larger groups of mechanical tissue occur on either side of the leaf.

Reproduction. The plants are usually **dioecious** but some of the species deserve mention in that they are not strictly dioecious and possesses some **abortive ovules** in the male flowers. The male and female cones are organized to form an **inflorescence** of the panicle type, though in some cases terminal cones are often met with (Fig. 161 A). The panicles usually arise in the axils of foliage leaves, which fall off before the cones develop, hence the conebearing branches are leafless. The male and female cones are several cm. long and consist of a stout **axis** which bears at base two opposite, sterile and connate leaves (**bracts**) with acute apices. A little higher up, a number of circular bracts are superposed above one another at each node forming a cup surrounding the axis. These have been called by Vimla Vasil (1959) "**collars**" or "**cupules**". Due to the supression of internodes, the collars lie very close to each other. Each cone shows 10-25 such collars. In some abnormal cones the collars are arranged spirally.

Male Cone. The male cone has more than a dozen (about 15) collars. Above each collar, there are three to four definite **rings,** each of about 25 30 male flowers. (Fig. 161, C). Just above the male flowers lies a ring of nearly ten to fifteen reduced, functionless female flowers with abortive ovules. But Thompson (1916) reported more than one ring in *G. gnemon*, whereas Pearson (1914) has described pure male flowers without infertile ovules in *G. africanum* and *G. buchholzianum*. Each **male flower** consists of a **stalk** bearing two unilocular **anthers** enclosed in a sheath-like annular **perianth** (Fig. 165). Sometimes, there are present one, three or four anthers instead of two anthers. When mature, the stalk of the anther elongates rapidly pushing the anthers through a **slit** in the perianth beyond the collars of the cone (Fig. 161, D).

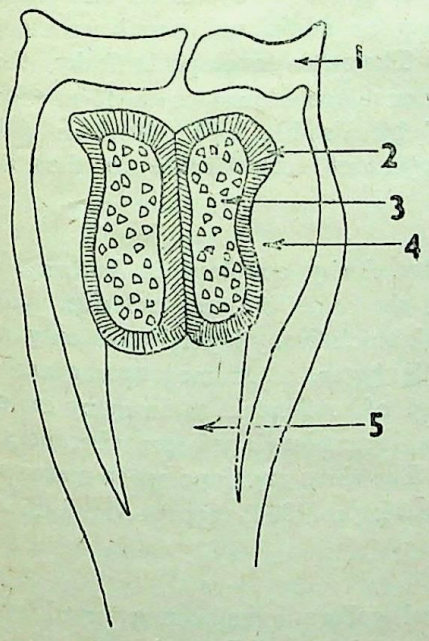

Fig. 165. L. s. of male flower of Gnetum before dehiscence 1, Perianth; 2, wall of microsporangium, 3, Microspores; 4, Unilocular anther, 5, Stalk.

While very young, the cones are completely enclosed within two basal bracts. Later on the cone

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axis is seen with the collars closely addressed to each other. Longitudinal sections reveal that some cells all round the axis below each collar become **meristematic** and undergo many divisions to form a ring like swelling known as **annular meristem.** This annular meristem differentiates into 10—15 **ovular buds** on the upper-side, and 25—30 **male flower primordia** on the lower-side. The male and female rings are separated by a few **sterile cells** from which a large number of **epidermal hairs** arise. The cells lying below the first ring of male flowers undergo subsequent meristematic divisions so us to fom four rings of male flowers. At this stage the ovular buds become prominent showing a massive outer, an imperfect middle and a persistent inner envelope surrounding a nucellus.

According to Pearson (1912) an annular mucilage canal appears in the collar in *G. buchholzianum* and *G. africanum* but not in *G. ula.*

Female Cone. These resemble the male cones except that here a **single ring** of female flowers is seen above each collar. Each ring has got 3—10 ovules (Fig. 161, E). Each ovule represents a female flower. The ovules are **dimorphic.** The smaller ones degenerate, whereas some of the topmost collars are ovule-less. Each female flower or ovule consists of a **nucellus** (megasporangium) surrounded by **three** envelopes. Some ovules like those of *G. ula* show an additional fourth envelope (Vasil 1959 ; Lignier and Tison 1913). The **outer** envelope is **fleshy,** the **middle** is **sclerotic** (stony) and the **inner** envelope elongates to form "**the micropular tube**" or the socalled '**style**' by Vasil (1959). Maclean and Ivimey Cook (1952) regard this an 'integument' comparable to that in other gymnosperms.

According to Vasil (1959), the outer fleshy envelope is known as "**perianth**" and possesses **stomata** on the outside and **sclerids** and **laticiferous ducts** in the mesophyll. This thick fleshy layer leaves only a narrow opening at the top. The middle layer, after megasporogenesis divides in its upper region forming a sort of bottleneck. In many cases cells lying at the tip of this middle layer develaped protuberances. Stomata and Sclerids are present here. The third envelope when matures becomes brown and finally black. Waterkeyn (1954) reports the formation of a fringe-like structure from this.

Abnormal female cone with spiral collars have been reported by Thompson (1916), Gonzalves and Landwa (1951) and Dutt (1952).

During the development of the ovule an **annular meristem** arises below each collar like that of the male cone. From this arise 8-10

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ovular primordia separated by sterile cells which form hairs in a manner exactly similar to that of the male cone. The ovular primordium arises on a cushion from which the three envelopes develop in centripetal succession.

When mature the ovule shows an orange red outer envelop with a hard ridged middle layer. The inner black layer on drying breaks down. The 'perianth', middle envelope are free from each other right from the base while the inner enevelope is fused with nucellus atleast in the basal part. The 'perianth' is of uniform thickness whereas the middle integument widens out towards the **micropyle**. These two envelopes form a complete covering around the ovule.

The morphology of these three envelopes had long been a matter of dispute. According to Strasburger (1872) all these develop by the differentiation and splitting of the usual single integument, like other gymnosperms. But this is not supported by facts. Beccari (1877) suggested that the outermost envelope is a perianth or something analogous to it and the two remaining envelopes are integuments. This view was supported by Coulter (1908).

Vimla Vasil (1959) in case of *G. ula* reports that the inner envelope which develops micropylar tube aborts in some cases. In such cases, the middle envelope elongates to form a normal-looking micropylar tube (the 'style').

Microsporogenesis. A group of **hypodermal** archesporal cells differentiate in the young anther. These divide periclinally to form a **parietal layer** and a mass of **sporogenous cells.** The parietal layer forms the **anther wall** which comprises of a persistent epidermis, a single middle layer and tapetum. The last two are gradually absorbed and hence the persistant epidermis shows **fibrous thickenings** resembling those of the endothecium of angiosperms. The **sporogenous cells** undergo a few divisions to produce **microspore mother cells.** These contain dense cytoplasm and prominent nuclei. When nearing meiosis, their protoplasm recedes from the mother wall and a new mucilagenous layer is developed between the wall and the protoplasm. The reduction divisions are simultaneous producing decussate isobilateral or tetrahedral tetrads. As the microspores enlarge, the mucilaginous wall is absorbed and the mother wall breaks down releasing the microspores. Each young **microspore** is provided with a thick spiny **exine** and a delicate **intine.** Dehiscence of the anther takes place by means of a **longitudinal slit** which extends vertically from the tip to some distance below the anther-sac on each side (Fig. 161, IV.)

Male Gametophyte. We owe a lot to Negi and Madhulata (1957) who have given the details of the male gametophyte of *G. ula* which we

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unknown. The microspore divides to form a small lenticular **prothallial cell** anda **larger cell** (Fig. 161, III). The nucleus of the larger cell divides to form two daughter nuclei. Gradually one of them becomes comparatively larger than the other sister nucleus and has a prominent nucleus. This is known as tube nucleus, whereas the smaller deep staining nucleus which lies near the prothallial cell and has a sheath of its own, is called **generative nucleus**. (161, I IV). All workers on *Gnetum* are of the opinion that the mature pollen grains are **3—nucleate**, excepting Karsten (1893) who mentioned 2-nucleate condition and Vasil (1959) who has observed four nuclei as abnormalities in *G. ula*. The nature of these three nuclei has long been a subject for discussion. According to Pearson (1912 : 1914) there are the **prothallial, generative** and **tube nuclei,** while Thompson (1916) regards them to represent **tube nucleus, the stalk and body cells** (Fig. 266). According to Negi and Madhulata (1959) the present view is that both in *G. ula* and *G. gnemon,* there is a **prothallial cell,** a **tube nucleus** and **a generative cell.**

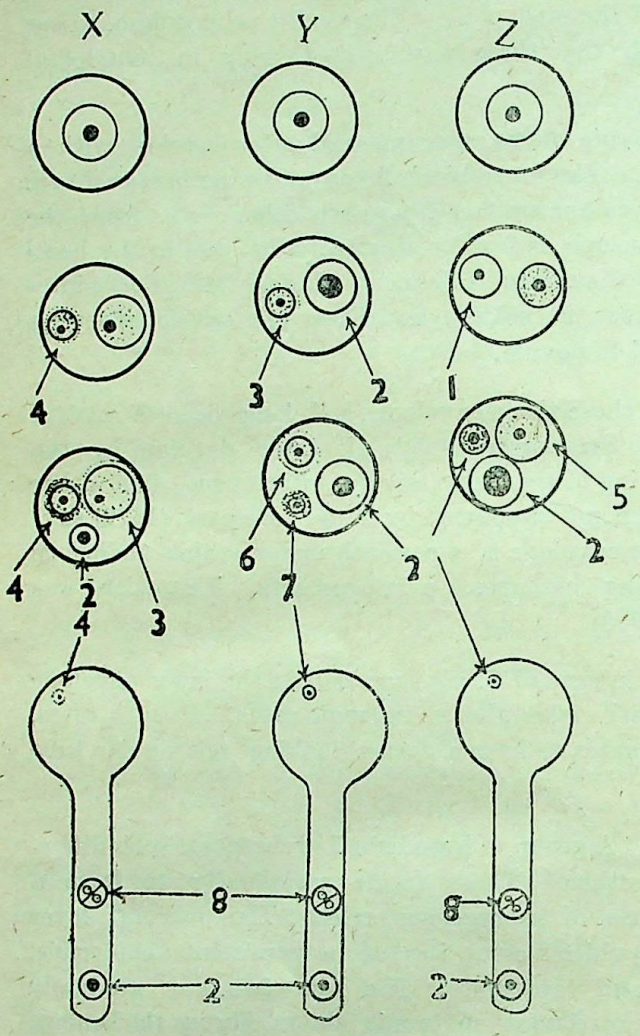

FIG. 166. Diagrammatic representation of the various views of the development of the male gametophyte of *Gnetum*. *X*, Present view ; *Y*, Thompson's view ; Z, Pearsons' view ; 1, Prothallial nucleus; 2, Tube nucleus ; 3, Generative cell ; 4, Prothallial cell; 5, Generative nucleus; 6, Body cell; 7, Stalk cell; 8, Male cells.

Vasil (1959) has observed some double pollen grains which were uni-, bi-, or tri-nucleate in nature.

Megasporogenesis. The ovule shows one to three hypodermal **archesporial cells** in the nucellus. These divide periclinally forming the

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parietal and **sporogenous** layers. The sporogenous cells divide once or twice to form 8 10 **megaspore mother cells** (Fig. 161, F). Vasil (1959) reports that occasional archesporial cells may function directly as a megaspore mother cell without cutting off a parietal cell. The development of the female gametophyte shows all the three types, the **mono-**, **bi-**, and **tetrasporic** development as reported by Lotsy 1941, Thompson 1916. Fagerlind 1941, Apte and Kulkarni 1953, Waterkeyn 1954. Negi and Madhulata (1957) have confirmed Fagerlind and Waterkeyn's obser-

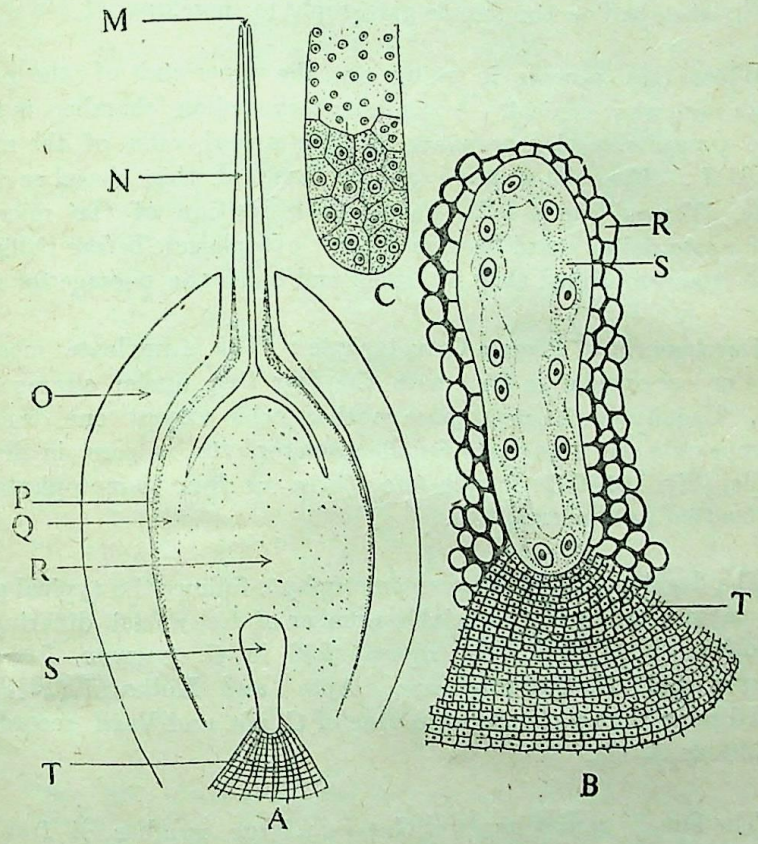

FIG. 167. Pavement tissue and female gametophyte of *Gnetum*. *A*, L. s. of ovule showing deep-seated embryo-sac ; *B*, Embryo sac with well developed nutritive "pavement tissue" ; *C*, Mature embryosac showing formation of prothallial tissue at the antipodal end ; (*M*, Micropyle ; N, Inner covering forming long stylar canal'; *O*, Outer fleshy layer; *P*, Middle stony layer ; *Q*. Inner fleshy layer ; *R*, Nucellus ; *S*. Embryo sac. *T*, Pavement tissue).

vations in *G. ula* and *G. gnemon* regarding the tetrasporic orgin of the embryo sac of *Gnetum* This angiospermous feature deserves mention because it has not been soen in any of the Gymnosperm except *Gnetum*.

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Usually the imperfect ovules on the male cones do not develop beyond this stage (megaspore mother cell stage). But works of Lotsy 1899, Pearson 1914, Thompson 1916 indicate that in *G. gnemon* and *G. africanum* these may occasionally develop in a normal manner to give rise to seeds.

While the megaspore mother cells are preparing for meiosis, some of the cells of the nucellus lying below them divide to form the so-called "**pavement tissue**" which becomes conspicuous during the development of female gametophyte (Fig. 167). The nutritive "*pavement tissue*" is gradually absorbed as the female gametophyte develops.

When this process is going on, the upper end of the nucellus becomes somewhat conical. A rudimentary pollen chamber is formed by the progressive degeneration of the apical cells of the nucellus (Fig. 161 J). The cells situated at the base of this chamber develop **papillae**. The epidermal cells of the middle portion of the micropylar tube elongate radially and become densely cytoplasmic before pollination. After it is accomplished they interlock and block the passage for ever.

Development of Female Gametophyte : The 4-nucleate megaspore is more or less ovoidal in form with the four free nuclei aggregated in centre. Usually all the megaspore mother cells except one degenerate and hence only one 4 nucleate female gametophyte is seen in the ovule as a rule, (Fig. 161, GII) though two, three or four gametophytes have been reported as abnormalities.

The development of female gametophyte follows the typical gymnosperm pattern producing a variable number of free nuclei differing with the species. Thompson (1916) reports 256 in *G. gnemon,* 512 in *G. molucence* and *G. leptostachyum*, Apte and Kulkarni (1953) have reported more than a thousand in case of *G. ula*, and Vasil records more than 1500 *in G. ula*.

The female gametophyte with a very large number of free nuclie takes up an inverted flask like form with a broad upper portion and a long narrow basal portion (Fig. 161, G IV). At this stage, **cell-formation** begins at the base of the gametophyte developing **endosperm** and gradually proceeds upwards (Fig. 161, J). Mention must be made of the fact that the cell formation never reaches beyond the base of the upper expanded part, hence this portion remains free nuclear. The endosperm consists of uninucleate and multinucleate cells.

By this time pollination takes place and a few pollen tubes can be seen inside the gametophyte (Fig. 161. J). At this stage 2-4 groups of 3 to 8 richly cytoplasmic cells differentiate in the upper free nuclear part. These

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develop in the vicinity of the pollen tubes. One or two cells in each

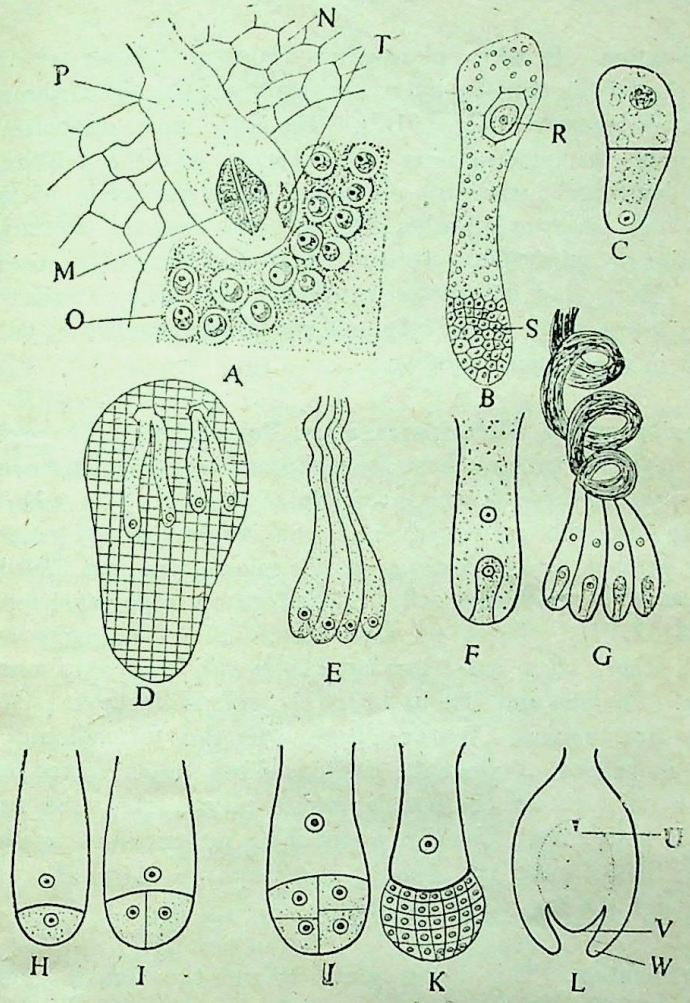

FIG. 168. Fertilization in *Gnetum* and development of embryo. *A*, Fertilization showing differentiation of oosphere nuclei (O) in the embryo sac and pollen tube containing two male cells (M) and a tube nucleus (T); *B*, Embryo sac after fertilization showing zygote and cellular part of female gametophyte; *C*, First division of zygote to form the suspensor tubes; *D*, Later stage showing cellular female gametophyte (endosperm) in which a number of primary suspensor tubes develop; *E*, Primary suspensor tubes coil; *F*, Development of "Peculiar cell" in the suspensor tubes; *G*, late stage and seed shedding stage; *H—K*, Development of embryo from the "peculiar cell"; *L* Mature embryo showing differentiation into stem-tip, radicle and cotyledons; (*M*, Male cells; *N*, Nucellar tissue; *O*. Oosphere nuclei; *P*, Pollen tube; *R*, Zygote; *S*, Cellular part of female gametophyte; *T*, Tube nucleus; U, Radicle; *V*, Stem tip; *W*, Cotyledon).

group function as eggs (Fig. 168). According to Vasil (1959) the egg and

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its cytoplasm, in *G. ula* are separated from the rest of the female gametophyte by a definite wall.

Pollination. It takes place when the ovule shows about 200-250 nuclie in the female gametophyte. At this stage the tip of the micropylar tube becomes lacerated (Fig. 161 J). The is the most opportune time for the lodging of the pollen grains which are caught in a pollination drop. After pollination the radially elongated epidermel cells of the middle portion of the micropylar tube interlock and seal the micropyle. The pollen grains or microspores are sucked in and reach the socalled pollen chamber. Here they germinate rupturing the exine, so that the intine comes out into a short **pollen tube.** A very large number of pollen grains germinate in the pollen chamber.

Development of Microspores after Pollination. The pollen tube develops near the tube nucleus from the microspore. It grows into the nucellus passing through the intercellular spaces. The tube nucleus is the first to enter the pollen tube and this is followed by generative cell while the prothallial cell remains in the microspore and finally disorganises there. The **generative cell** divides forming two **equal** male cells in *G. ula* (161, I VII). These are also functional if two eggs are present near each other. But according to Thomson (1916) only one of them functions. Pearson and Thomson (1917) and Waterkeyn (1954) believe that they are unequal. Watever it is, after the formation of two male cells the movement of the tube nucleus slows down, hence by the time the pollen tube enters the female gametophyte, the tube nucleus lies behind the male cells. Usually about 2-10 pollen tubes are seen in the nucellus. These enter the female gametophyte latterally or in some cases through the apex (Fig 161, J).

Fertilization, This takes place when the female gametophyte shows about 700—800 free nuclei a cellular endosperm at the base and a few eggs. Usually I-4 pollen tubes are seen in a female gametophyte. According to Thompson (1916) the pollen tube bursts at the periphery of the female gametophyte, but this has not been observed by Vasil (1959) in *G. Ula*. The male cells are released when the eggs are differentiated from the free nuclei. Karsten (1913) observed the fusion of male and female nuclei in *G. ovalifolium* and *G. rumphianum*. Vasil (1959) observed **normal fertilization** in *G. ula* but it is completed in very short time unlike the findings of Thompson (1916) in *G. leptostachyum* where it takes a very long time. The result of fertilization is the formation of a **zygote** which gets surrounded by richly cytoplasmic cells of the endosperm (Fig. 161 K).

After fertilization, many of the free nuclei degenerate and the remaining show wall formation thus forming endosperm in this micro-

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pylar region as well. The endosperm assumes on oval form and its main bulk is produced from the lower necklike part of the female gametophyte, hence the older stages show a broader zone at the base and a narrow zone above.

Development of Embryo : The large zygote has got dense cytoplasm and a prominent nucleus. Usually 1-4 zygotes may be seen in one female gametophyte. The stages of the zygote development are highly controversial. In *G. ula* as reported by Vasil (1959) the zygote neither develops directly into suspensor tube as reported by Lotsy (1899) in *G. gnemon*, nor undergoes any free nuclear divisions as shown by Karsten (1893) and Pearson and Thomson (1917) in *G. ovalifolium*, *G. rumphianum* and *G. africanum*, and Coulter (1908) in *G. gnemon*. Instead the **zygote** divides followed by wall formation to form **two cells** (Fig. 161, L) Apte and Kulkarni (1953) reported the formation of a mass of cells instead of two cells. The two cells produced by the first division of the Zgyote elongate to form **primary suspensor tubes** (Fig. 161, M). Each is a uninucleated structure. These primary tubes give rise to **secondary tubes** by cell divisions. These tubes grow mainly towards the basal nutritive region of the endosperm and in doing so get coiled to form a bundle (Fig. 161, N).

At the tip of each tube is cut off a "**peculiar cell**" after which the seeds are shed from the female cone and the further development of the embryo takes place in the soil (Fig. 161 O). It is from this 'peculiar' cell that the entire embryo is derived. The **embryonal cells** enlarge at the expanse of the endosperm, which grows in such a way as to produce a conical structure – the **plumule** at the end of the embryonal mass. The cells on either side of the plumule divide to form two orange pink **cotyledons** of same size but in exceptional cases they may be unequal. Opposite the plumule, the embryo differentiates into the **radicle** (Fig. 161 R*i* R)

After the differentiation of the cotyledons, a small peculiar hump like tissue develops from the hypocotyledonary region of the embryo. This has a well-developed vascular supply and is the most important noteworthy feature of the emhryo of *Gnetum* and is called the "**feeder**". This "feeder" shows the histological differentiation of tissues into epidermis, cortex, vascular bundles and pith. The "feeder" though shorter than the hypocotyl in the beginning ultimately outgrows it. By this time both the primary and secondary suspensors have been absorbed and are reduced to minute thread-like structures. These get attached to the root cap The mature embryo shows the presence of laticiferous ducts and sclerids.

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Mention must be made of the fact that a few interesting cases show the development of **lateral roots** from the **pericyclic region** of the radicle prior to the germination of the seed. Such abnormal cases of special interest have been recorded by Bower (1882) and Haining (1920) in *G. gnemon* and Apte and Kulkarni (1953) in *G. ula*.

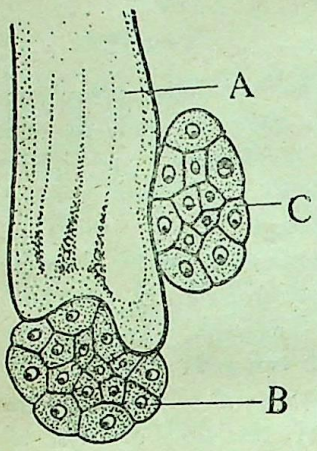

FIG. 169. Polyembryony in *Gnetum*; *A*, Primary suspensor tube; *B*, Normal embryo; *C*, Secondary embryo.

Polyembryony is of common occurrence in *Gnetum* and may take three ways as mentioned below, but only one embryo matures, the remaining disappear (Fig. 169).

(a) A normal embryo may develop at the tip of primary suspensor tubes.

(b) The embryonal mass at the tip of secondary suspensors proliferates to develop new larges sized additional embryos.

(3) In some cases, such as *G. ula*, **supernumerary embryos** may develop from any meristematic point in secondary suspensors. Such meristematic regions may produce buds or chains of cells which organise into new embryos which can hardly be differentiated from the normal embryso.

Economic Importance :

Food. Seeds of *G. gnemon* are eaten after boiling or roasting. The orange or red pulp of the fruit is removed and the seed kernel washed and moulded into cakes, dried in sun and fried in boiling oil into a kind of cake or biscuit. Young leaves and inflorescence are cooked in soup or eaten as vegetable. Seed kernel of *G. contractum*—a Travancorian species yields oil which is used for edible purposes.

Medicine. The seed kernel of *G. contractum* yields a fixed oil which is used in Travancore for massage in rheumatism. *G. montanum* possesses piscicidal properties. In Annam the roots and stems are used as antiperiodic.

Ropes and Nets. The bark of *Gnetum* yields a strong durable fibre with good tensile and breaking strengths. It is used for making ropes and nets. The fibre is used for fishing lines. Ropes mades from this are strong, pliable and light.

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Paper. Fibre of *G. gnemon* is suitable for paper manufacture.

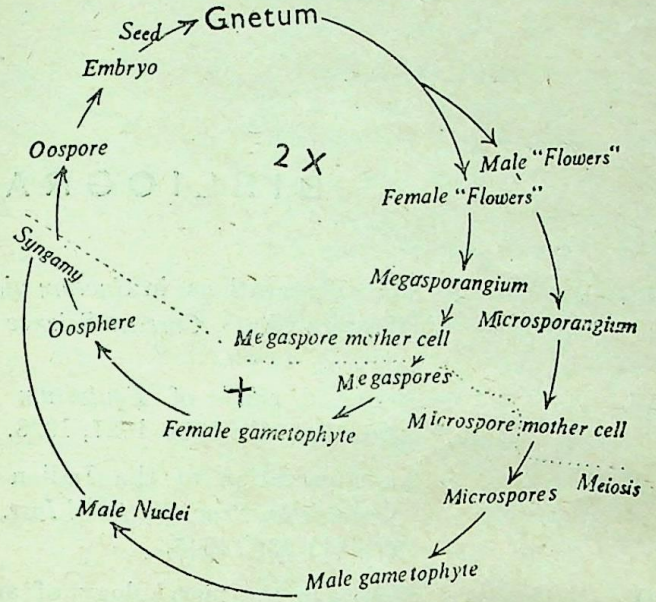

FIG. 170. Life Cycle of *Gnetum*.

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INDEX

The numerals stand for page numbers.

A

Actinostele, 200
Aerenchyma, 161
Algal zone, 219
Albumious cells, 240
Amphiphloic siphonostelic, 161
Amphithecium, 19
Antheridia, 2, 25, 49
Andreales, 5
Androgonial cells, 15, 50
Androcyte mother cells, 15
Androcytes, 15
Anthocerotales, 5
Anthocerotae, 33
Anthoceros, 33; structure, 34; reproduction, 34, sexual, 35; development and structure of antheridia, 36; development and structure of archegonia, 38; fertllization, 39; post fertilization stages 40; structure and germination of spores, 42; life cycle, 43; species A. erectus, A. himalayausis, A. chambensis, A. gollani, A. longii, A. dixithi. A. sahyadrensis, A. crispulus, 34.
Annulus, 68, 142, 194
Anthophyta, 205
Annual rings, 246
Anemophilous, 257
Annular meristem, 272
Apical cell, 101
Apophysis, 70
Apogamous embryos, 196
Apophysis, 229
Archegonia, 2, 49
Arnold, 3
Archegoniatae, 4
Arthophyta, 134
Archesporium, 40, 53
Archegonium initial, 16, 120, 125
Aril, 256
Atavism, 118
Autonomous 238
Axis, 142

B

Bark, 240
Basal cell, 16
Blepharoplasts, 150, 236
Body cell, 236
Bryan, 52
Bower, 44,
Bract scale, 255
Buffer cell, 228
Bulbils, 117, 228
Buxbaumiales, 5,

C

Calyptra,
Calamites, 208
Calyptra, 151
Cambium, 228
Campbell, 44
Capsule, 2,
Carinal canals, 138
Casparian strips, 113, 141
Calobryaceae
Caulonema, 72
Cauline, 118
Centroxylic, 114
Centripetel, 223
Centrifugal, 223
Chaetophorales, 4,
Chlorophyceae, 4, 5,
Chloronema, 72
Christmas trees, 241

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Digitized by Arya Samaj Foundation Chennai and eGangotri

Chemotactic, 173
Clevage polyembryony, 262
Cladogenous, 107
Coal measures, 83
Coleorhiza, 238
Cork, 240
Collars, 271
Cupules, 271
Columella, 41
Cycadales, 213
Cycas, 215; distribution, 215; habit and external vegetative character, 215; anatomical structure, 217–228; veg. reproduction, 228; sexual reproduction, 229; male cone, 229; development of microspores and germination upto pollination 231; female cone, 231; megasporangium or ovule, 238; development of megaspore and female gametophyte, 233; germination of megaspore and development of female gametophyte, 233; pollination, 235; development of Male gametophyte after pollination, 236; Fertilization, 236; development of embryo, 237; seed; germination of seed, 238; economic importance, 239; Coniferales, 240; important characteristics of the group, 240; economic importance, 241; classification, 242

D

Dawsonia, 1
Diarch, 217
Diaphragm, 124
Dimorphic, 111, 118
Dioecious, 140, 215
Dictyosteles, 155
Direct traces, 220
Diploxylic, 225
Diphasium, 91
Dixon, 5, 45
Double fertilization, 205

E

Ectophloic siphonostele, 202
Elaters, 145
Embryo sac cell, 233
Endothecium, 19
Endosperm jacket, 235
Endospore, 123
Equisetales, 133
Equisetum, 133; external characters of sporophyte, 134; anatomical structure, 135-140; reproduction, 141; development of sporangium, 144; germination of spore and development of gametophyte, 147; development of archegonia, 148; development of antheridia, 149; fertilization, 150; development of embryo, 150; economic importance, 15; life cycle, 154
Eusporangiate, 118, 156
Eubrya, 56
Exine, 101
Exogenous, 107
Exospore, 123
Eustele, 137, 202

F

Funaria, 57; occurrence, 57; species F. fascicularis, F. muehlenbergii, F. attenuata, F. obtusa F. hygrometrica, 57; structure 58; reproduction, 59; development and structure of antheridium, 61; development of the archegonioum, 63; fertilization, post-fertilization stages, 65; detailed account of the development of capsule, 66; development in the central fertile region 66; development in the apical region of the capsule, 68; development in the lower region of capsule, 69; disposal of spores, 70; alternation of generations, 75; life cycle, 75
Feeder, 279
Fertilization, 125
Filicales, 156
Filicineae, 155; classification, 156

G

Gemmae, 23
Generative cell, 231; 274; 278
Geological time, 214
Genotypic, 43

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Digitized by Arya Samaj Foundation Chennai and eGangotri

Gnetales, 265
Gnetum, 266 ; geographical distribution, 266 ; external vegetative characters, 267 ; anatomical structure, 269-270 ; reproduction, 271 ; male cone, 271 ; female cone, 272; microsporogenesis, 274 ; development of female gametophyte, 276 ; pollination, 278 ; development of microspores after pollination, 278 ; fertilization, 278; development of embryo, 279 ; polyembryony, 280 ; economic importance, 280 ; life cycle, 281
Gradate sori, 157
Girdle trace, 220
Gymnospermae, 207 ; habit, 207 ; internal structure, 208 ; reproduction, 208 ; classification, 209-211

H

Halle, 4
Hadrome, 48
Halophytes, 155
Haplostele, 200
Haplocherelic, 266
Haskall, 3
Hauperzia, 91
Haustorial end, 236
Hepaticae, 1, 2, 7
Heteroblastic, 32
Heterotrichous, 74
Heterosporous, 85, 118
Heteropory, 147
Heterophyllum, 111
Homeophyllum, 112
Homosporous, 85
Hor etails, 132
Hyalodermis, 47
Hypocotyl, 238
Hypodermis, 250

I

Inflorescene, 256
Innocuous parasites, 220
Intine, 101

J

Jacket initial, 50, 120
Jungermanniales, 5

L

Leaftrace, 198
Leaflet cycas, 224,
Lianas, 268
Living fossil, 229
Liverworts, 7,
Lycopodiales, 91
Lycopodiaceae, 91
Lycopodium, 91; species of L. selago L. qloifolium, L. phlegmaria, L. clavatum, L. inundatum L. complanatum, 92 ; internal structure, 94—96 ; vegetative propagation, 97; Reproduction, 98, sporangia, 99; development of gametophyte, 99; development of antheridium, 104 ; development of the archegonium, 104; developmept of embryo, 105; life cycle, 108; economic importance 109 ; ligule, 162.
Leptosporangiate, 156

M

Marchantia, 21, structure, 22; gemmae, 23, reproduction, 24; antheridiaphore and antheridia 25; archegoniophore and archegonia 26 ; fertilization and post-fertilization stages 27; germination of spore, 31 ; species M. polymorphe, M. palmate, M nepalensis M. simlana, 22 ;
Marchantiaceae, 20
Marchantiales, 8
Marsilea, 157 ; distribution and occurrence 157; external characters of the sporophyte, 158; internal structure, 160—163 ; internal structure of sporocarp, 163—165; morphological nature of sporocarp, 165; bursting of sporocarp & liberation of sori, 167; development of sporangia, 168; microspore and development of male gametophyte, 168; megaspore and development of female gametophyte, 170; fertilization, 173; development of embryo, 173; life cycle, 175.
Marginals, 156
Male flower, 272

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Digitized by Arya Samaj Foundation Chennai and eGangotri

Manoxylic, 222
Medulla, 48
Megaspores, 85, 118
Megahhyllous, 155, 231
Medullary ray, 269
Megasporangium, 118
Mesarch, 189
Microspores, 85, 118
Melin, 52
Microsporangium, 118
Monophyletic, 90
Monarch, 113
Monoecious, 147
Mixed protostele with pith, 201
Musci, 1, 2,
Mucilaginous, 273
Micropyle, 273
Mycorrhiza, 245

N

Neck, 85
Neck canal cells, 85
Nucellus, 208
Nucellar beak, 238

O

Octant stage, 106
Oogamous, 2
Oospore, 75, 85, 128
Oophyte, 85
Operculum, 54
Opercular cell, 194
Organ suigeneris, 115
Osmunda, 186 ; distribution and occurrence, 186; Habit and external characters, 187; anatomical structure, 188—191; Vegetative propagation, 191 ; reproduction, 191; germination of spore, 194; development of antheridium, 194; development of archegonium, 195; development of embryo, 196 ; features of special interest, 197;

P

Paracutlerees, 89
Papillae, 176
Paranuclei, 260
Pavement tissue, 276
Palisade, 162
Pericycle, 162
Precocious, 129
Perispore, 145
Peristomial layer, 68
Peristome, 70
Perianth, 271
Pinus, 243; distribution, 243; habit and external vegetation characters, 243: anatomical structur 245—252; reproduction, 253 microspore and development o male gametophyte, 254; mal cones, 253; microspore an development of male gameto phyte, 254; female cone, 255 ovules 256; pollination, 257 further development of mal gametophyte, 257; developmen of female gametophyte, 259 fertilization, 260; developmen of embryo, 262; dispersal of seed 263; germination of seed, 265 life cycle, 264.
Pipes, 132
Pith, 139
Pinnules, 159
Phylloglossacees,
Phylloglosum,
Phyllosperms, 210
Plasmodium, 168
Plectostele, 201
Plumule, 238
Pollination, 127
Polyarch, 114
Polystelic, 114
Polyarch. 115
Polycyclic stele, 198; 202
Polyembryony, 209
Pollen tube, 278
Pteropsida, 155, 211
Pteridophyta, 83; habit and habitat 84; anatomical structure, 84 reproduction, 85; Classificatio 86, 87, 88; origin of, 88:
Prohepatics, 4, 89
Pteridium, 175; occurrence, 175 habit and external characters 176; internal structure of rhi zome, 179:—leaf, 178; reproduc tion, 179; development of spo rangium, 177; dehiscence of cap sule, 180; germination of spore and formation of prothallus, 18 development of antheridium

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181; development of archegonium, 183: fertilization, 184; post-fertilization stages and formation of a new plant, 184; life cycle, 185.
Protonema, 43,
Prothalli, 85
Prolycopodinees, 89
Protopteridophyta, 89
Protandrous, 122
Prothallus, 125
Protostelic, 152, 188
Pseudomesarch, 224
Pseudopodium, 54

Q

Quadrant, 151

R

Riccia, 10 ; Ricciaceae, 9 ; Riccia fluitans, 1, 13 ; Ricciocarpus natans, 1, 10 ; Reilla, 1 ; R. vesicata, R. bulbifera, R. glauca, R. crystallina, R. robusta, R. frostii, R. pathankoteusis, R. discolour, R himalayansis, R. Sanguinea, R. Bischoffii, R. curtisii, 13 ; Vegetative reproduction, 13 ; Sexual, 13 ; development of antheridium, 15 ; development of archegonium, 15 ; fertilization, 17 ; Post-fertilization stages, 17 ; structure & germination of spore, 20 ; life cycle, 20
Rachis, 222
Resin canal, 245
Rhizophore, 113
Royal fern, 187

S

Sargassum, 4
Sago palm, 215
Scandent, 111
Sclerids, 272
Scouring rushes, 132
Selaginella, 110 ; distribution and occurrence, 110 ; species : S. lepidophylla, S. rupestris, S. oregana, S. pygmea, S. gracillima, S. kraussiaua, S. chrysocaulos, S. krysorhizos, S. pallidissima, S. sanginolenta, S. jacquemonth, 111 ; external characters of sporophyte, 111 ; Structure of sporophytic plant, 114-117 ; reproduction, 117 ; distribution of micro-and megasporangia, 118 ; germination of spores, 121 ; mechanism of sporangial dehiscence, 122 ; development of female gametophyte, 122 ; fertilization, 125 ; development of embryo, 128 ; features of special interest, 129 ; life cycle, 131.
Selaginellales, 110
Secondary suspensor tubes, 279
Sequoias, 240
Seed, 203
Seed habit, 127
Siphonostele, 201
Siphonogamy, 205
Simplices, 156
Siphonostelic, 137, 152
Silica, 135
Smith, 45
Solenostele, 198
Sphagnobrya, 45
Sphagnum, 46 ; occurrence, 46 ; structure, 47 ; rhizoids, stem, 47 ; leaves, 48 ; reproduction, 49 ; development and structure of archegonium, 51 ; fertilization, 52 ; post-fertilzation stages, 52 ; germination of spore, 55 ; life cycle, 55.
Sporogenous tissue, 53
Sperms, 85
Spur branches, 244
Spathulate gametophyte, 194
Spermatophyte, 203 ; reproduction, 204, classification, 205
Sporocarp, 162 ; internal structure, 163 ; transverse section, 164 ; longitudinal section, 165 ; morphologial nature, 165
Sporophore, 167
Sperms, 150
Sporangia, 141
Strobili, 141
Solenoxylic, 114
Stamens, 265
Starchgrains, 222
Stachyosperms, 210

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Stelar system in ferns, 198-202
Style, 272
Suspensor, 128
Subsidiary cells, 136
Suspensor cell, 106
Supernumery embryos, 280
Syndetocheilic, 266
Symbiotic, 219
Symbiotic mycorrhiza, 100

T

Tapetum, 144, 193
Tetrarch, 217
Terpentine, 250
Tetrasporic, 275
Thalassiophyte, 89
Timber, 241
Trabeculated endodermis, 113
Transfusion tissue, 228, 252
Tube cell, 255
Tubers, 162

U

Urostachaceae, 91

V

Vaginule, 54
Vallicular canal, 136
Venter, 85
Venter canal cell, 85
Vertical, 173
Vernation, 178
Vessels, 269

W

Walton, 3
Wing, 263

X

Xerophytes, 155, 208
Xerophytic, 226
Xylem, 190

Z

Zygote, 173

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